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LETHAL GENE-COMBINATIONS AND POLLEN STERILITY IN DIPLOID APPLE VARIETIES

A CRITIQUE AND A THEORY

BY *OTTO HEILBORN*
STOCKHOLM

INTRODUCTION.

IT is a well established fact that different apple varieties show great differences with regard to the fertility of their pollen. The degree of pollen fertility of a given variety has hitherto always been determined by means of germination tests. These germination tests are generally carried out by sowing the pollen-grains in a cane sugar solution (generally 10 %) and counting those grains that germinate. The result of such a test is then given in a figure representing the number of germinated pollen-grains expressed in per cent of all grains counted. Tables of such *germination percentage* figures for the pollen of hundreds of apple varieties have been published by several authors (conf. R. FLORIN 1920, 1926, 1927, ZIEGLER and BRANSCHEIDT 1927 and KOBEL 1931 as well as the literature there given).

Pollen germination tests of a given apple variety may give different results in different cases, and the germination percentage tables published thus often give the impression of very great variability within many of the apple varieties investigated. The explanation of this variability within the varieties as well as the differences found between them seemed to require a cytological investigation of the pollen development of the apples. Such investigations were, therefore, undertaken, some years ago, by several workers almost simultaneously (SHOEMAKER, KOBEL, RYBIN and HEILBORN, conf. HEILBORN 1928) and have more recently been taken up by NEBEL (1929 a and b) and DARLINGTON and MOFFETT (1930). One of the most significant results of these cytological studies is the establishment of the existence of quite a series of triploid apple varieties. All these triploid varieties have bad pollen, as shown by its very poor germination. All the diploid varieties have 34 somatic chromosomes, the triploid ones have 51. The reduction division of such triploid varieties is irregular.

The reduction division of a diploid variety, again, is normal under normal and ordinary conditions. The quite conspicuous variability found by germinating pollen of diploid varieties thus required some other explanation. It was quite natural to seek for such an explanation in climatic influences. In fact, I have myself been ablo to state that the chromosome conjugation in the pollen mother-cells of certain diploid apple varieties is sensitive to high temperatures (HEILBORN 1928, 1930). I have, however, not as yet been able to prove any clear parallelism between chromosome conjugation and pollen germination. In order to produce a further elucidation of this problem, I therefore, in the spring of last year (1930), placed some dwarf trees of a few apple varieties in one of the heated green-houses of Hortus Bergianus at Stockholm, and then investigated both the reduction division and the pollen sterility of these varieties, thus put under the influence of a rather high temperature (in the daytime about + 30° C.). I am greatly indebted to Messrs C. FLORIN and E. SÖDERBERG for the loan of these dwarf-trees.

When the flowering of the dwarf trees had ceased, in 1930, the trees were again transplanted into the open air. There they were left for the summer of 1930 and the following winter, and during spring of this year (1931) the investigation on chromosome conjugation and pollen sterility was carried out once more, now under normal conditions of temperature and moisture. The details of these investigations have not yet been fully worked out and will be published later, nevertheless, a few facts appear to be quite clear already now. *The reduction division as well as the fertility of the pollen are not much influenced by changes in temperature, provided these changes are kept within moderate limits.* Moreover, *the differences between the apple varieties, as regards their pollen fertility, seem to reappear each year, independent of climatic changes, and in spite of the normal chromosome conjugation generally prevailing.* These facts at once suggest the real explanation of the differences in pollen sterility, displayed by diploid apple varieties. Most probably *this sterility depends upon certain lethal gene-combinations present in some apple varieties, and absent in others.*

POLLEN VIABILITY AND GERMINATION.

Why, now, have not these lethal gene-combinations been discovered by those workers that have investigated the sterility of apple pollen? Obviously because almost all tests hitherto carried out with

apple pollen, have been *germination* tests, resulting in the determination of percentage figures of germination. The percentage of pollen-grains, actually germinating during the experiment, depends, however, on two different categories of factors, partly on the properties of the pollen itself, partly on the conditions prevailing during the experiment. The temperature, for instance, exercizes a great influence on the germination of the pollen. To these two categories of factors influencing the germination of the pollen — the genetically founded properties of the pollen itself and the external influences on the germination process — due regard has not been paid by any of the authors dealing with this problem. *This is one reason why the real sterility differences between diploid apples have not hitherto been observed,* and do not appear from a study of the germination percentage tables as yet published.

When the present writer began his study on the pollen of the above-mentioned dwarf trees, the necessity of thus distinguishing between the internal properties of the pollen and the external influences, soon became apparent. Instead of determining the *germination percentage* of the pollen under investigation, I therefore determined another constant which in the following will be referred to as the *viability percentage* (or germinability instead of germination percentage). It was found that *a part of the apple varieties investigated constantly contain a rather high amount of abortive pollen-grains that are empty*, lacking living plasma and nucleus. These abortive grains do not swell in cane sugar solution, as do the viable grains, and often have a somewhat navicular shape (perhaps reminding of stomata; fig. 1 *b*—*c*). In diploid apple varieties it is generally quite easy to distinguish betweeen viable and abortive pollen-grains. As viable are regarded such grains as have actually germinated, as well as all those which have attained about the same size and shape as the germinated grains, though no pollen tubes have been developed. Abortive grains are those which show the characteristics mentioned above. The *viability percentage* is then the number of viable pollen-grains, expressed in per cent of the total number of grains counted. — Before counting I sowed the grains in a 10 % cane sugar solution, in the same way as is generally used in germination tests.

As has been mentioned above, the abortive and the viable pollen-grains of diploid apples are generally easily distinguished from one another. The viable grains all seem to be capable of germination if the conditions are favourable. The abortive grains, of course, do not

germinate, as they are empty. The classification of the pollen-grains, suggested in the preceding, must consequently be regarded as representing essential properties of the pollen of diploid varieties. With regard to the pollen of triploid apples, however, the new classification fails. Fig. 1 *c* shows some pollen-grains of the triploid variety »Ribston». One of the grains is empty and of the same shape as the abor-

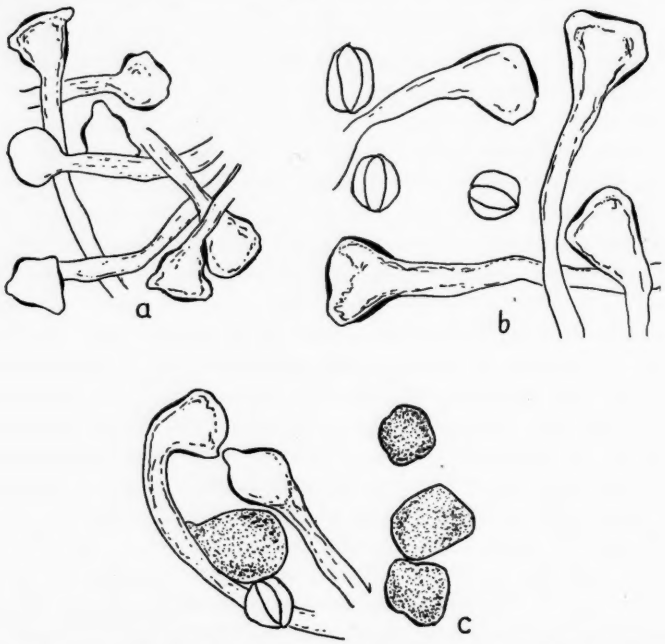

Fig. 1. Pollen of apple varieties. *a*: »Signe Tillisch» (group *A*: all grains viable). — *b*: »Melon» (group *B*: 4 viable and 3 abortive grains). — *c*: »Ribston» (triploid: 2 viable grains, 1 abortive, and 4 grains containing plasma but not germinating). — Obj. 7 a, oc. 2.

tive grains of the diploid varieties, two grains appear to be normal and have germinated, the rest of the grains have attained a somewhat normal size, though they are of a more or less irregular shape, but have not germinated. Though these last-mentioned grains have not germinated, they have a rich content of plasma, and some of them may be capable of germination under special conditions. In the case of triploid apples, the classification into viable and abortive grains does not, therefore, give a proper idea of the real properties of the pollen —

nor does the classification into germinated and non-germinated grains. *One reason why the significance of the abortive grains in the pollen of diploid apples has not before been observed, is obviously due to the circumstance that diploid and triploid varieties have not been separated from one another during the germination experiments.* The difficulty of classifying the pollen of triploid apples has, therefore, prevented a proper classification of the pollen of the diploids. Studies on apple pollen must, consequently, always be combined with cytological studies on the chromosome set of the varieties investigated.

R. FLORIN (1920, p. 17) says: »Bei den Sorten, deren Pollen nur zu einem geringen Prozent (20 oder darunter) keimfähig war, befanden sich neben den gesunden Körnern teils zahlreiche taube, zusammengeschrumpfte, teils häufig Körner, die freilich nicht taub waren und demnach Schwellen zeigten, wenn sie in Zuckerlösung ausgesät wurden, die aber dessenungeachtet nicht keimten. Interessant wäre zweifelsohne eine Untersuchung über die Morphologie des Pollens bei den Obstbäumen vorzunehmen, die möglicherweise gewisse Aufschlüsse über die genotypische Konstitution der einzelnen Sorten würde gewähren können». The author obviously seems to have overlooked the important circumstance that empty pollen-grains occur, not only in varieties with a very low germination percentage (*i. e.* triploid varieties!), but also in many of those varieties with relatively good pollen, which we now know to be diploids.

In a similar way ZIEGLER and BRANSCHEIDT (1927) have observed morphological differences between the pollen-grains in many of the varieties investigated, but these authors, too, have failed in distinguishing between diploid and triploid varieties. They note if the pollen investigated is »gleichmässig» or more or less »ungleichmässig», though without percentage figures. The last-mentioned characteristic is attributed to chromosome aberrations.

Later on, BRANSCHEIDT, in a recent paper (1930, p. 372 f.), has devoted a chapter to the morphology of the pollen of apples and grapes. In all the twelve apple varieties in table 1 of this paper he found empty pollen-grains. In some of the varieties there was, moreover, found a further class of pollen-grains, characterized by BRANSCHEIDT as »bedingt keimfähig». The last-mentioned grains were not empty, but in spite of their plasma and nucleus they did not germinate in the experiments, though they were regarded as capable of germination under favourable circumstances. BRANSCHEIDT is obviously still ignorant of the existence of triploid apple varieties, otherwise he must have observed

that »bedingt keimfähige» grains occur in the triploids only, not in the diploid varieties of his table 1. Moreover, he regards the *size* of the pollen-grains as their most significant characteristic and presents curves of pollen-grain sizes in which the different morphologic kinds of grains are not properly separated from one another, nor are the diploid from the triploid varieties. These curves do not, therefore, give much information as to the essential relations between pollen morphology and pollen germination. The percentages of empty grains in the diploid apple varieties presented in BRANSCHEIDT's table 1, are, however, very useful for our present purpose (though they are founded on rather scanty statistics — generally only 120—150 pollen-grains for each variety). Some of BRANSCHEIDT's data have, therefore, been included in the present paper and shall be discussed later (table 2, p. 10).

KVAALE (1927), too, observed empty pollen-grains in many apple varieties and made a few countings of their frequency, but also he did not separate the triploid varieties from the diploids, and as the number of grains counted in each variety moreover seems to be very low, KVAALE had no more success than the other workers in finding the real significance of the empty grains. He attributed the origin of the empty grains to »irregularities in the division of the pollen mother-cells».

When thus the proper way of testing the pollen of diploid apple varieties must consist of its classification into viable and abortive grains, and when the abortion of the pollen is regarded as depending on certain lethal combinations of genes, there remains now the most important task to reinvestigate the pollen of all diploid apple varieties from our new point of view. I began this work during the spring of this year (1931), and my scanty preliminary results may be published already now in order to give a fuller idea of the problem. Attention should, in this connection, be paid to the following theoretical point of view. If the abortion of the pollen depends upon certain lethal combinations of genes, these gene-combinations must be assumed to be limited in number. In other words, one might expect the diploid apple varieties to be divided into a few distinct classes — representing the gene-combinations — when classified according to the viability percentages of their pollen.

In table 1 the viability percentage figures of 15 diploid varieties are given, together with some data on the germination of the pollen, presented by previous authors. All the apple trees investigated in the present paper grow in Hortus Bergianus at Stockholm. As to the names

TABLE 1. *Viability (determined 1931) and germination of pollen of diploid apple varieties.*

Apple variety	2n	Grains counted		Viability percentage	Group	Germination percentage					
		Good	Empty			Florin 1920 [1]	Florin 1926	Florin 1927	Johansson 1929	Ziegler and Branscheidt 1927 [1]	Kvaale 1927
Cox's Pomona	34	934	16	98	*A*	96	76—96	71—100	96	—	98
Oranie	34	922	8	99	*A*	94	92—97	71—100	87	—	—
P. J. Bergius	34	864	13	99	*A*	27	73—94	71—100	—	—	—
Signe Tillisch	?	805	16	98	*A*	92	64—92	71—100	—	—	86
Sävstaholm	34	—	— [2]	98	*A*	90	85—93	71—100	95	—	64,8
Vitgylling	34	743	11	99	*A*	—	—	—	—	—	—
Yellow Richard	34	1369	24	98	*A*	78	77—78	71—100	—	79	—
Alexander	34	698	66	91	*B*	9	50—91	71—100	—	—	66,4
Astrachan, white, specimen I		1009	105	91							
Astrachan, white, specimen II		1035	182	85							
Astrachan, white, total	34	2044	287	88	*B*	30	30—83	31— 70	85	92	62,8
» , big, transparent	?	564	130	81	*B*	11	60—77	71—100	—	—	—
Charlamovsky, specimen I		404	26	94							
Charlamovsky, specimen II		1117	79	93							
Charlamovsky, total	34	1521	105	94	*B*	49	49—89	—	—	96	87,3
Melon	34	1200	293	80	*B*	75	70—75	—	90	—	—
Åkerö	34	828	136	86	*B*	90	70—90	71—100	77	—	42,2
Björkvik	?	517	342	60	*C*	53	—	31— 70	—	—	—
Cellini, specimen I		737	519	59							
» , » II		677	434	61							
» , » III		643	250	72							
» , total	34	2057	1203	63	*C*	92	60—92	71—100	—	93	88,1

[1] Maximum values.

[2] Determined 1930 (figures lost!).

of the varieties I have relied upon the determinations made by the staff of the garden.

As is seen, there occurs a good deal of variability as regards the germination of the pollen, which does not exist to the same degree in the viability percentage figures. This variability in germination is

partly real, depending upon varying germination conditions, partly only apparent and depending on the circumstance that *all the previous authors, working on apple pollen, seem to have counted too few pollen-grains for the determination of each percentage figure.* Few of the authors give any details in this respect, it is, therefore, for instance, impossible to calculate the mean value of percentage figures given by different authors, nor is it possible to compare the results obtained in different germination experiments. It is, of course, erroneous to calculate mean values of different percentage figures of germination without knowing the numbers of germinated and non-germinated grains actually counted in each experiment. Such a way of calculating has, however, obviously been practized by some of the authors cited in the present work.

R. FLORIN (1920) merely says in the introduction to his work that he has counted about 300 pollen-grains for each percentage figure in his tables. JOHANSSON (1929) counted »at least 200», ZIEGLER and BRANSCHEIDT (1927) generally about 300, often 400—500 grains. From table 1 in KVAALE's work (1927) we learn that for each of those percentage figures that have been included in our table 1, KVAALE had counted a number of grains varying from 65 to 126. KOBEL, finally, in his most recent work (1931) says that at least 200—300 pollen-grains should be counted for the determination of a germination percentage figure. In all these works the number of grains counted appears to be too low, at least in all cases of an intermediate germination (when both pollen classes, consequently, constitute about half of the total number counted). Although I have not made any statistical studies on this point, I am under the impression that 1000 or 2000 grains should be counted for the determination of each percentage figure. *A good deal of the variability in pollen germination reported by previous authors and partly attributed to climatic or metabolic influences, is most probably but apparent and in reality depending upon insufficient statistics.* — In table 1 I have, accordingly, also given the actual numbers of viable and abortive grains counted in each test. In each of the slides investigated I have counted the good and the empty grains in a considerable number of different fields.

VIABILITY CLASSES.

Though the apple varieties whose pollen viability percentage has been determined are as yet few, the figures published in table 1 are sufficient to show that there exist at least two, perhaps three, viability

classes among diploid apple varieties, and that the variability in pollen sterility is much less irregular than the germination figures of the previous authors indicate. About half the apple varieties investigated have a practically quite fertile pollen — its viability is never lower than 98—99 %. The empty grains, occasionally found in these varieties, should be attributed to mere casualties. The percentages of those varieties which show a greater amount of abortive grains, are variable, though not to the same extent as the germination percentage figures of previous authors. Most of these viability percentage figures range from 80 to 94, the pollen of two of the partially sterile varieties (»Cellini» and »Björkvik») show, however, a viability, in my experiments, that is no higher than 63 and 60 % respectively. I am under the impression — though I have not yet been able to convince myself of it — that there is a more marked difference between the pollen classes of the two last-mentioned apple varieties than between the corresponding classes of the others: the abortive grains make an impression of being slightly smaller and narrower. All facts taken together, therefore, make it feasible that »Cellini» and »Björkvik» really may belong to a sterility class of their own.

We should thus be able to classify the diploid apple varieties into three classes as regards their pollen viability: class *A*, good pollen (viability 98—99 %); class *B*, inferior pollen (viability 80—94 %); and class *C*, fairly bad pollen (viability 60—63 %). It is, however, not yet quite certain that the classes *B* and *C* really can be separated from one another.

From table 1 it thus becomes evident that a proper comparison between the pollen of different varieties cannot be based upon percentage figures for germination, determined without due regard being paid to the amount of empty pollen-grains, characteristic of each variety, and without a very strict control of the conditions prevailing during the germination experiments. The grouping of the varieties into fertility classes, made by FLORIN (1927) and arranged so that these classes show continuous transitions (0—30, 31—70 and 71—100 % of germination — only the two last-mentioned represented in table 1), may, perhaps, be useful from a practical point of view, but scientifically it is not quite fortunate, as this arrangement only makes the real differences between the varieties still less clear. On the whole, it is quite obvious that the percentage figures for germination, hitherto published, do not show clearly more than one thing, *viz.* the profound difference between triploid and diploid varieties. KOBEL (1931, p. 115)

has also taken the consequences and divides the apple varieties into only two groups, instead of three, *viz.* good and bad pollen producers, the last-mentioned consisting of the triploid varieties.

TABLE 2. *Viability and germination of pollen of apple varieties.* (*According to* BRANSCHEIDT *1930, table 1, rearranged and simplified.*)

Apple variety	2n	Empty grains %	»Bedingt keimfähige Körner» %	Viability percentage (»Keimfähig»)	Group	Germination percentage
Grahams Jubiläumsapfel	?	2,0	—	98,0	*A*	95
Roter Trierer Weinapfel	?	1,9	—	98,1	*A*	90—98
Wintergoldparmäne	?	1,8	—	98,2	*A*	94—99
Landsberger Renette	?	13,4	—	86,6	*B*	87
Ontario	34	21,8	—	78,2	*B*	72
Danziger Kantapfel	34	58,8	—	41,2	*C*	43
Grüner Fürstenapfel	?	40,7	—	59,3	*C*	54
Gravensteiner	51	93,9	—	6,1	Triploids	0—10
Goldrenette von Blenheim	51	15,6	63,1	21,3		0—20
Jakob Lebel	51	50,0	40,0	10,0		5—12
Pollinger Klosterapfel	?	62,2	1,7	36,1		30—42
Schöner von Boskoop	51	53,4	19,3	27,3		7—20

From his experiences of pollen germination in cherries and pears KAMLAH (1928) draws the following conclusion: »Aus diesen Feststellungen folgern wir, dass die bisher in der Literatur angegebenen schlechten Keimer in 2 Gruppen zerfallen, und zwar in solche, die einen tatsächlich degenerierten Pollen besitzen, und die infolgedessen nicht in der Lage sind, hohe Keimprozente zu erreichen, und in andere, die nur zufällig in die Gruppe der schlechten Keimer geraten sind, weil ihnen optimale Keimungsbedingungen gefehlt haben». These words once more demonstrate the lack of accuracy of the current germination tests. As has just been shown, the apple varieties fall into three or four groups of the kind referred to by KAMLAH (groups *A*, *B*, *C* and the triploids).

In table 1 of the paper by BRANSCHEIDT (1930), referred to above, some interesting data on the morphology of apple pollen are found which are presented in table 2 of the present work. From BRANSCHEIDT's table the data on pollen-grain sizes have been omitted, but instead of

these the chromosome numbers of the varieties investigated have been included in so far as they are known. Moreover, all data have been rearranged in order to give a better survey of the whole. One experiment with »Schöner von Boskoop» has been omitted, because it does not supply any clear information as to the classification of the pollen, and the three experiments with »Landsberger Renette» have been brought under one heading.

As is seen, BRANSCHEIDT's results agree remarkably well with my own. BRANSCHEIDT himself, however, has not understood the importance of his observations, obviously because he has not treated the diploids and the triploids separately. On the whole, he seems inclined to attribute all differences in pollen morphology to chromosome aberrations. This cannot be correct.

If tables 1 and 2 are considered together, we arrive at the following results regarding partial pollen sterility in diploid apples: of 22 varieties investigated, 10 are wholly fertile (class *A*), 8 show a moderate pollen sterility (class *B*), and 4 are pollen sterile to a considerable degree (class *C*).

When the greater part of the present paper had already been written, the author came across a quite recent book by KOBEL (1931) in which the sterility phenomena of cultivated fruits are reviewed and discussed. On p. 127 of this work KOBEL says: »Mit der zytologisch bedingten und der durch mangelhafte Ernährung verursachten Pollensterilität haben wir wohl noch nicht alle Ursachen für die Degenerationserscheinungen des Pollens erfasst. Es gibt wohl Obstsorten, die auch bei normalem Chromosomensatz und guter Ernährung viele verkrüppelte Pollenkörner ausbilden. Zu diesen gehört wahrscheinlich die Apfelsorte Tobiäsler, die den normalen Satz von 34 Chromosomen enthält, deren Pollen aber stets, und auch an gesunden und kräftigen Bäumen, zahlreiche Krüppelkörner aufweist. Wir gehen wohl nicht fehl mit der Annahme, dass es sich hier um *faktoriell bedingte* Sterilität handle, d. h. dass ein Teil der Pollenkörner Erbanlagen erhalte, durch welche ihre Entwicklungsfähigkeit verunmöglicht werde. Ein sicherer Nachweis dieser Sterilitätsform, die bei anderen Pflanzen mehrfach gefunden wurde, konnte allerdings noch nicht erbracht werden, und ist schwer zu erbringen».

These words contain the only clear statement which the present writer has found in the literature on sterility of cultivated fruits, respecting the possible existence of a pollen lethality caused by certain gene-combinations and independent of chromosome aberrations and

external influences. KOBEL has not, however, made any further investigations on this problem and obviously regards the final proof of such a lethality as a very difficult task. As will appear from the present paper, the easiest way of proving this »faktoriell bedingte» pollen sterility is to prove, by way of sufficient statistics, the existence of distinct *sterility groups* among diploid fruit varieties.

LETHAL GENE-COMBINATIONS AND POLLEN ABORTION.

Genetically analysed cases of partial pollen sterility, caused by lethal gene-combinations without chromosome aberrations, are few. To these belong the cases of *Stizolobium* (BELLING 1914), *Galeopsis* (MÜNTZING 1929, 1930), *Datura* (BLAKESLEE 1928) and *Zea mays* (BRINK 1927 and BRINK and BURNHAM 1929). In all these cases the inheritance of the partial sterility is interpreted in terms of simple Mendelian gene-combinations. The interpretation of the *Stizolobium*-case thus requires two independent pairs of genes, and that of *Galeopsis* four such pairs. The interaction of such genes results, in certain crosses between different pure lines, in the appearance of partially sterile individuals in the off-spring, in regular Mendelian proportions. The partially sterile individuals have a certain amount of their pollen aborted. According to the simple Mendelian gene-combinations, underlying this abortion, the abortive grains always constitute about $^1/_2$ or $^1/_4$ of the total number of grains. If a population of *Galeopsis*-individuals of such line-crosses is investigated, the individuals, consequently, may be arranged in a limited number of sterility groups. One of these groups will show 50 % and one 25 % of pollen abortion, while the third group will consist of wholly fertile individuals.

Other cases of such partial pollen sterility are found in *Oenothera* (RENNER 1919, LEHMANN 1922), but as all inheritance phenomena in this genus are very complicated, it seems difficult to interpret the *Oenothera*-cases in quite simple terms.

As it is bound to be extremely tedious and lengthy to investigate the pollen sterility of apples by means of bastardizing experiments, I have tried, in the present investigation, to establish the existence of lethal gene-combinations by collecting statistics on the pollen sterility of a number of diploid varieties. The apple varieties of our gardens may be regarded as a population of individuals which has arisen as the result of previous line-crosses. Now, as has just been shown, it is,

in fact, possible to divide this population into distinct sterility groups, and thus our supposition that relatively simple gene-combinations are responsible for the partial pollen sterility in diploid apples, is confirmed.

The existence of a great class of apple varieties that quite lacks pollen sterility (class *A*) does not appear from a study of the germination percentage tables, hitherto published. This discovery is of importance, as a distinct group of quite fertile apple varieties must, of course, be supposed to exist, if the hypothesis of lethal genes be accepted. *These lethal gene-combinations are lacking within class A.*

FLORIN (1927, p. 112) says: »— — there is no sharp distinction between presence and absence of good pollen, and many grades of pollen abortion occur in both pears and apples. Any one variety appears to be characterized by the production of a certain quantity of pollen with a more or less constant range of abortion and degree of viability. Thus pollen sterility is obviously in the first place an inherent characteristic». The last-mentioned observations concerning the hereditary nature of pollen sterility in apples and pears, is no doubt correct, on the other hand the very first remark about the lack of distinction between presence and absence of good pollen (or of bad pollen!), is not adequate. There really exists a sharp distinction between wholly fertile and partially sterile apple varieties.

The explanation of the rather irregular percentage figures of viability of classes *B* and *C* is not so simple. An excellent possibility of explanation has, however, recently been given by DARLINGTON and MOFFETT (1930). These authors have found the »diploid» species and varieties of *Pyrus* to be, in reality, »secondary diploids», possessing a balanced secondary chromosome set, regarded as a combination of two primary sets. These secondary diploids should be tetraploid with regard to a part of their chromosome set and hexaploid in respect of the rest of it. The chromosome constitution of the apples is consequently: *AAA BBB CCC DD EE FF GG* (haploid set). *Quadrivalent and sexivalent chromosomes are often found in meiosis.*

If we now assume a recessive lethal gene *d* to be situated in a *D*-chromosome, and then assume further that such recessive lethals are effective only if present in both *D*-chromosomes of a pollen-grain, we get the following formula for the constitution of an abortive pollen-grain: *AAA BBB CCC dd EE FF GG.* We may also assume that the two *d*-genes of a partially sterile apple variety are situated each in one of the two *D*-pairs of chromosomes, that, consequently, such an

apple variety with two *d*-genes in its chromosome set has two chromosome pairs *D—d*, *D—d*. If the chromosomes of one pair always mate and sort independent of the other pair, $^1/_4$ of the pollen-grains will be double recessives *dd*, and the viability of the pollen will be 75 % (fig. 2 *a*). If, on the other hand, the two pairs are always united to such a quadrivalent chromosome as is suggested in fig. 2 *b*, so that the *d*-chromosomes always go together (as if they were one single chromosome), $^1/_2$ of the pollen-grains will be double recessives *dd*, and the viability of the pollen will be 50 %. Intermediate frequencies of such quadrivalent chromosomes will result in percentage figures of viability, ranging from 50 to 75 %. This type of pollen viability would correspond to class *C*.

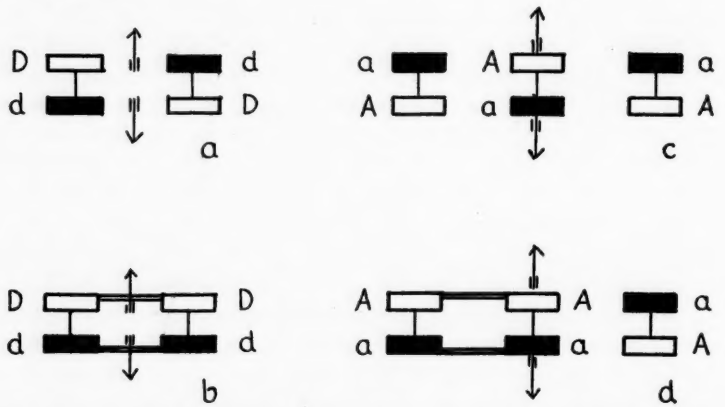

Fig. 2. Diagram of the behaviour of homologous chromosome pairs in meiosis of diploid apples. Chromosomes carrying a recessive lethal gene are drawn black. *a*: Chromosome pairs *D—d* independent of one another: gametes *DD* + 2 *Dd* + *dd* (75 % viability). — *b*: Chromosome pairs *D—d* united to a quadrivalent: gametes *DD* + *dd* (50 % viability). — *c*: Chromosome pairs *A—a* independent of one another: gametes *AAA* + 3 *AAa* + 3 *Aaa* + *aaa* ($87\,^1/_2$ % viability). — *d*: Two chromosome pairs *A—a* united to a quadrivalent, the third pair *A—a* independent: gametes *AAA* + *AAa* + *Aaa* + *aaa* (75 % viability). — Conf. the text.

We may also suggest the recessive lethal genes to be situated in the hexaploid part of the chromosome set, *e. g.* in the *A*-chromosomes. If a lethal *a*-gene is effective only when present in all three *A*-chromosomes of a pollen-grain, an abortive grain of this type has the following constitution: *aaa BBB CCC DD EE FF GG*. Further, we may, as above, suppose the *a*-genes to be situated each in one of the three pairs of *A*-chromosomes of a partially sterile variety of this type, all these pairs

thus to be *A*—*a*. If the chromosomes of each of the three pairs now always mate and sort independent of the chromosomes of the other pairs, $^1/_8$ of the pollen-grains will be triple recessives *aaa*, and the viability of the pollen will be 87 $^1/_2$ % (fig. 2 *c*). If, again, two of the three pairs always form a quadrivalent chromosome of the type suggested in fig. 2 *d*, so that the two *a*-chromosomes of this quadrivalent always go together, while the third chromosome pair is independent, $^1/_4$ of the pollen-grains will be triple recessives *aaa*, and the viability of the pollen will be 75 %. If only in some of the pollen mother-cells such *A*-quadrivalents are formed, the viability of the pollen will become intermediate between 75 and 87 $^1/_2$ %. The pollen viability of class *B* might, perhaps, be of this type.

However, the viability percentages of group *C* might perhaps also be interpreted as indicating merely simple half-sterility, and those of group *B* $^1/_8$-sterility, with modificatory deviations of an unknown nature.

The above explanations of the pollen sterility of classes *B* and *C* are, of course, only suggestions. It is futile to try to explain the sterility in detail, so long as the viability percentage is not known of a much greater number of apple varieties. In the above lines the author only wishes to point out the important fact that the compound structure of the apple chromosome set, discovered by DARLINGTON and MOFFETT, is in very good consonance with the irregular viability figures of the partially sterile diploid apple varieties. *The best proof of the correctness of our new explanation of the pollen sterility in diploid apples lies, however, as yet in the fact that this sterility is totally lacking within a whole group of apple varieties* (class *A*).

CRANE and LAWRENCE (1931) publish tables with germination percentage figures (determined by other authors) for such apple varieties as have been investigated cytologically. From these tables it appears that the germination of the pollen of triploid varieties varies between 4 and 27 %, and that of diploid varieties between 46 and 98 %. Corresponding figures, published by KOBEL (1931, p. 109), are, for triploids 4—34, and for diploids 50—97. From such figures we might conclude that diploids never contain less than 50 % of good pollen — in excellent consonance with our new gene theory of pollen sterility in diploid apples.

CONCLUSIONS.

The most important *conclusions* that may be drawn from our new view on pollen sterility in diploid apples, are the following. *There is*

a sharp distinction between wholly fertile and partially sterile varieties, of which only the first-mentioned should be regarded as perfect pollen producers. The sterility has a genetical basis and is, to a high degree at least, independent of climatic or metabolic conditions.

The new theory set up in the preceding may serve as the foundation of a new programme for future work on pollen sterility in apples. This work should be a combination of *chromosome* studies and studies in pollen *viability*. First, the chromosome number of all apple varieties of horticultural value should be determined, and in this way all triploid varieties recognized, and classified separately. The diploid varieties should then be investigated with regard to the viability percentage of their pollen. A more thorough knowledge of the causes of pollen abortion, as expressed in the viability percentages, might then perhaps be obtained through a study of the frequency of quadrivalent and sexivalent chromosomes in meiosis. It is possible that some relation may exist between the frequency of quadrivalents and sexivalents on one hand, and the viability percentage figures on the other. This last-mentioned conclusion may be drawn from the preceding theoretical discussion.

Studies in *germination* of apple pollen, on the other hand, belong to another category of problems. Such studies should be carried on in connection with the investigations in cross-sterility and cross-fertility of the different varieties. These pollen germination studies should be carried on chiefly with apple varieties of class *A*, *i. e.* with the best pollen producers, and should be arranged as series of germination tests in such a way that pollen of each variety is germinated under several different conditions. It seems to be of especial importance to make series of germination tests with pollen of each *A*-variety together with stigmas or styles of other apple varieties.

The investigations are still in progress, and further details will be published later.

Botanical Institute, University of Stockholm, July 1931.

APPENDIX.

Since going to Press I have received A. A. MOFFETT's paper »The chromosome constitution of the *Pomoideæ*» (Proc. Roy. Soc., B, Vol. 108, 1931). The peculiar compound structure of the chromosome set, found by DARLINGTON and MOFFETT to characterize the genus

Pyrus, is shown, in the new paper, to apply to all genera of the group *Pomoideæ*. The basic chromosome number in the whole group is 17, and secondary association of the chromosomes occurs in all species investigated, the maximum chromosome association in the »diploids» being three sexivalents and four quadrivalents. Thus the chromosome constitution *AAA BBB CCC DD EE FF GG* is common to all »diploids» of the whole group.

On the other hand, it is now stated that only part of the secondary association is true chromosome conjugation. The rest of it is merely »secondary pairing», *i. e.* some sort of attraction between homologous gemini, without physical connections. The frequency of true quadrivalents and sexivalents is varying — generally low — thus all facts that seem to be in accord with the viability figures of apple pollen.

In the light of these new data, J. CLAUSEN's recent criticism (Hereditas XV, p. 301, 1931) of DARLINGTON's and MOFFETT's conclusions loses its validity. CLAUSEN maintains that the above authors' »figures afford no conclusive evidence about hexasomes and tetrasomes in the pure species as *Pyrus floribunda* and *P. Ringo*», though they »do so for the cultivated types, which are very complicated hybrids». CLAUSEN seems to hold the view that multivalents in apples are due to segmental interchange between chromosomes rather than to polyploidy. This view is probably incorrect. — Partial sterility due to segmental interchange (conf. HÅKANSSON, Hereditas XV, pp. 17—61, 1931) is obviously a different phenomenon. Some of the cases of sterility, cited in the present paper, might perhaps be interpreted in both ways.

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ÜBER POLYPLOIDIE IN BEZIEHUNG ZU KLIMA, ÖKOLOGIE UND PHYLOGENIE

CHROMOSOMENZAHLEN AUS TIMBUKTU

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BOTANISCHER GARTEN, KOPENHAGEN

I. PROBLEME.

KÖNNEN äussere Einwirkungen eine erbliche Veränderung bei Organismen herbeiführen? Diese alte Streitfrage hat man seit JOHANNSEN am öftesten mit einem entschiedenen Nein beantwortet. Über die allgemeine Gültigkeit dieses Urteils bin ich bei Reisen in verschiedenen Gegenden der Erde, wo die Pflanzen unter extremen klimatischen Verhältnissen intensive Einflüsse ertragen müssen, in Zweifel geraten. Diese Zweifel näher zu begründen ist die Absicht vorliegender Arbeit. Erwähnte Reisen wurden teils in den kältesten, teils in den wärmsten und trockensten Klimaten der Erde durchgeführt, und unter diesen für die Pflanzen so harten Daseinsbedingungen habe ich die Aufmerksamkeit namentlich auf solche Arten gerichtet, die in polyploiden Formen auftreten. Es scheint, dass Polyploidie bei der Neubildung von Arten eine Rolle spielt. Da nun Polyploidie durch Einfluss äusserer Faktoren entstehen kann, werden wir direkt in die Frage über die eventuelle Bedeutung der äusseren Einwirkungen für die Artbildung hineingeführt.

Bei der Suche nach Material, das zur Klärung des erwähnten Problems beitragen könnte, wäre es darum zweckmässig Pflanzen solcher Gegenden der Erde zu untersuchen, wo der Kampf ums Dasein infolge harter Aussenfaktoren besonders scharf wirkt. Ich war in der günstigen Lage 1) die *Arktis* (Grönland, Island und die Faeröer) und 2) die südliche *Sahara* bereisen zu können. Beständig auf der Suche nach Polyploiden, bin ich nun zu den Resultaten gekommen, über die unten berichtet wird.

Schon 1922 begann ich auf den Faeröer meine Studien über *Empetrum hermaphroditum*, das eine interessante zwittrige, tetraploide Form des getrenntgeschlechtigen *E. nigrum* darstellt (HAGERUP 1927). Es ist kaum ganz richtig, *E. hermaphroditum* als selbständige Art aufzufassen, da es nicht mit neuen Genen bereichert ist, sondern nur mit

neuen Kombinationen derselben Genen. In diesem Zusammenhang ist es aber von besonderem Interesse, dass ein *erblich konstanter Typus* entstanden ist. *E. hermaphroditum* ist nämlich das einzige *Empetrum*, das man auf den gewaltigen Arealen Ostgrönlands vorfindet, wo *E. nigrum*, das hier überhaupt nicht vorkommt, also nicht beständig *E. hermaphroditum* neubilden kann.

Schliesslich sei nochmals hervorgehoben, dass das tetraploide *Empetrum* mit einer sehr wichtigen Eigenschaft von grossem pflanzengeographischen Interesse bereichert ist, indem es viel weiter nördlich gedeiht, als das diploide *Empetrum*. Es scheint, als ob die Chromosomenverdopplung der Art eine erhöhte »Vitalität» verliehen, und sie im Kampf ums Dasein widerstandsfähiger gemacht hätte, so dass es ihr möglich wurde neues Land in Besitz zu nehmen, das für die diploide Form unbewohnbar war.

Es scheint also, dass die Probleme der Polyploidie sowohl die Artbildungsfrage als auch pflanzengeographische Grundprobleme berühren könnten. Wir haben es also mit zentralen Aufgaben der Biologie zu tun und müssen versuchen ein möglichst vollständiges Beweismaterial herbeizuschaffen.

Um zu untersuchen, ob die bei *Empetrum* vorgefundenen Verhältnisse möglicherweise allgemeingültig sind, habe ich 1924—1925 zytologisches Material von *Bicornes* in Grönland eingesammelt, und dieses mit weiterem Material aus dem Botanischen Garten zu Kopenhagen ergänzt.

Hierbei ergab sich, dass sich die meisten der innerhalb *Bicornes* festgestellten Chromosomenzahlen (HAGERUP 1928) in eine schöne 6-Zahlenreihe einordnen lassen: 6×1; 6×2; 6×3; . . . . 6×8. In vier Fällen wurden innerhalb derselben Gattung solche Zahlen vorgefunden, die durch Verdopplung voneinander abgeleitet werden können. Es ergab sich da, dass es stets die Arten mit den höchsten polyploiden Zahlen waren, die am nördlichsten zu wachsen vermochten. Dieses Resultat stützt also die bei *Empetrum* angetroffenen Verhältnisse.

Falls meine Theorie richtig wäre, müsste man erwarten, dass, wenn grosse Kälte das Vorkommen von Polyploidie verursachen könnte, auch grosse Hitze eine entsprechende Wirkung besitzen könnte. In der Absicht nun auch den *Einfluss der Wärme auf Polyploidie* zu untersuchen, habe ich 1927—1928 eine Reise nach Afrika unternommen und in der südlichen Sahara, in der Umgebung der Stadt Timbuktu, zytologisches Material eingesammelt, in einem Gebiet mit einem der heissesten und unerträglichsten Klimas der Erde. Die Blütenknospen

wurden in CARNOY's oder NAWASCHIN's Flüssigkeit fixiert, und bei der Heimkunft haben sie sich als gut konserviert erwiesen.

Ich habe die meisten Arten um Timbuktu fixiert, besonders bin ich aber solchen Gattungen nachgegangen, die in zwei Arten vertreten waren, von denen die eine womöglich an einen trockneren Standort gebunden war als die andere. In manchen Fällen habe ich mich jedoch mit einem Vergleich mit solchen Arten begnügen müssen, die mir nur durch die Literatur bekannt waren; oder auch liess eine Chromosomenpaarung vermuten, dass eine polyploide Form ähnlicher Art vorlag wie im Falle von *Empetrum hermaphroditum*, der in Fig. 3 in meiner Arbeit von 1927 dargestellt ist. (Man muss sich doch eingedenk sein, dass viele polyploide Arten keine gepaarten Chromosomen besitzen.)

Nachstehend folgt eine Liste über die Chromosomenzahlen der untersuchten Arten, sowie eine kurze Beschreibung solcher Verhältnisse bei den Pflanzen, die für die Beleuchtung der vorliegenden Frage Bedeutung haben können. Die zum Vergleich benutzten Zahlen sind den von G. TISCHLER (1931) und L. O. GAISER (1930) veröffentlichten Listen entnommen, auf deren Literaturverzeichnisse ich mir übrigens hinzuweisen erlaube.

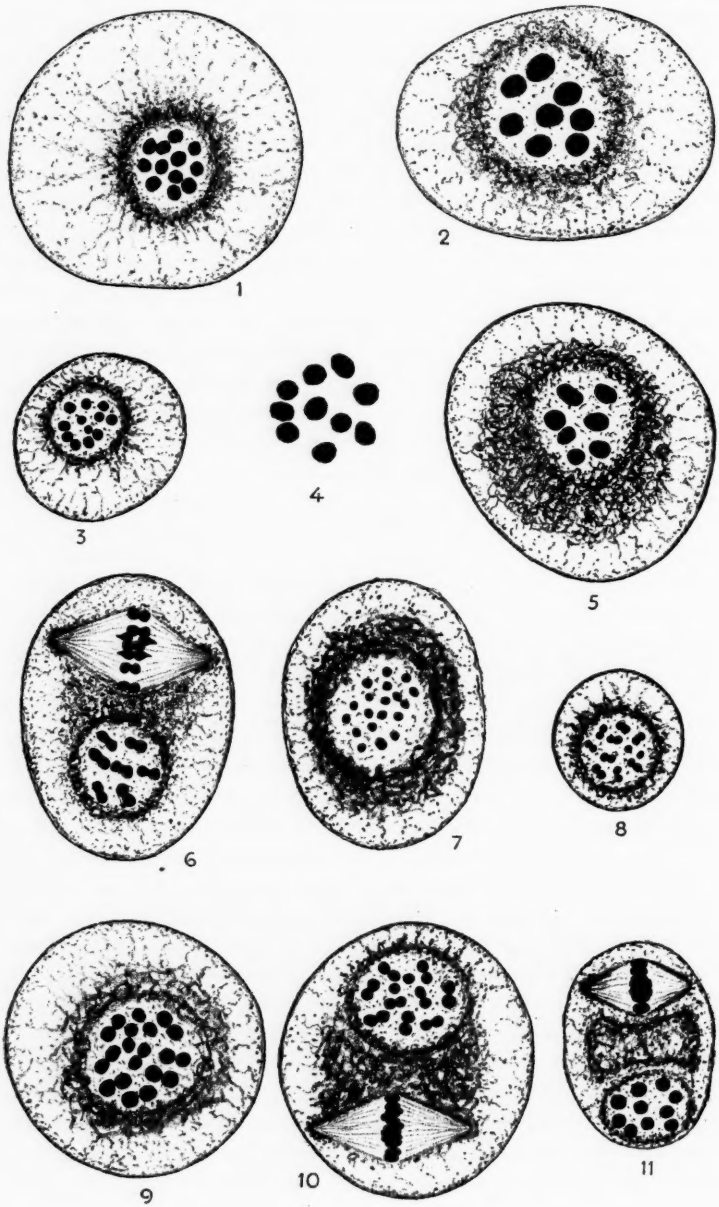
II. CHROMOSOMENZAHLEN AUS DER SÜD-SAHARA (TIMBUKTU).

Cucumis prophetarum L. (Cucurbitaceæ) ist eine typische Wüstenpflanze, die an den trockensten Orten zu wachsen vermag, wo sie am »glühenden» Sand niederliegt und mehrjährig ist. (Fig. 1; $n = 12$).

Cucumis melo hat ebenfalls $n = 12$, dagegen besitzt *C. sativus* $n = 7$ (KOZCHUCHOW). Ob *C. prophetarum* eine tetraploide Form einer der zahlreichen an feuchteren Orten vorkommenden, einjährigen Arten ist, lässt sich auf Grund des vorliegenden Materials nicht entscheiden.

Launaea integrifolia HAGERUP (Compositæ). Eine kleine Gattung typischer Wüstenpflanzen, von der man sonst keine Chromosomenzahlen kennt. In der nahestehenden Gattung *Lactuca* sind dagegen manche Arten mit $n = 5$, 8, 12, 16, 24 bekannt. Ein Grund, die Art als polyploid aufzufassen, liegt kaum vor. (Fig. 2; $n = 8$).

Farsetia ramosissima HOCHST. (Cruciferæ). Ein Zwergstrauch sehr trockner Orte. MANTON (in TISCHLER 1931) hat zwei andere Arten dieser Gattung mit $n = 7$—8 untersucht. Auf Grund des vorliegenden Materials lässt es sich aber nicht entscheiden, ob die Art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tetraploid ist; jedoch kommt $n = 6$ innerhalb der Cruciferen vor. (Fig. 3; $n = 12$).

Ricinus communis L. (Euphorbiaceæ). Diese Art, hierzulande als einjährige Pflanze angebaut, wird bei Timbuktu ein mehr als mannshoher mehrjähriger Baum. Mehrere Forscher haben an Wurzelspitzen europäischen Materials $n = 10$ gezählt. Ich habe Blütenknospen aus Afrika untersucht, die darlegten, dass die Pflanze in ihrer Heimat dieselbe Chromosomenzahl besitzt wie in Europa. (Fig. 4; $n = 10$).

Neurada procumbens L. (Rosaceæ). Diese typische Wüstenpflanze wurde schon von MURBECK (1916) untersucht, der $n = 6$ gefunden hat. Ich habe jedoch reichliches und gut konserviertes Material untersucht und niemals $n = 6$, sondern stets $n = 7$ festgestellt, was damit übereinstimmt, dass 7 die häufigste Grundzahl innerhalb der Rosaceen darstellt. Da MURBECK's Material jedoch aus andern Gegenden der Sahara stammt, können wir vielleicht mit zwei verschiedenen Rassen gearbeitet haben? (Fig. 5 und 6; $n = 7$).

Polygala triflora L. (Polygalaceæ). Dieser kleine Strauch wächst an sehr trocknen Orten. Die merkwürdige Zahl 19 lässt keine Polyploidie vermuten. Zum Vergleich habe ich *Polygala vulgaris* aus Dänemark untersucht, die sich in ihrer Reduktionsteilung jedoch so unregelmässig verhielt, dass ich die Chromosomen nicht zählen konnte. Auch sonst sind keine Chromosomenzahlen für die Gattung *Polygala* veröffentlicht. (Fig. 7; $n = 19$).

Capparis Rothii OLIV. (Capparidaceæ). Eine grosse, prachtvolle Liane, die ich bei Zinder in Französisch Nigeria an einem sehr trocknen Ort eingesammelt habe. In systematischer Hinsicht schliesst sie sich einer Gruppe von Arten an, die der Hauptart *C. corymbosa* LAM. sehr nahe stehen. Die Chromosomen liegen deutlich paarweise angeordnet (Fig. 8), was bedeuten kann, dass die Art tetraploid ist; ein Umstand, der vielleicht zur Erklärung des grossen Formenreichtums von *C. corymbosa* beitragen kann. Bei anderen *Capparis*-Arten hat KUHN $n = 9$, 15, 19, ca. 42 festgestellt. (Fig. 8; $n = 2 \times 10$).

Euphorbia granulata FORSK. (Euphorbiaceæ). Ein kleines, nieder-

Fig. 1—11. — *1*: *Cucumis prophetarum*. Heterotypische Metaphase. × 2300. — *2*: *Launaea integrifolia*. Heterotypische Metaphase. × 2000. — *3*: *Farsetia ramosissima*. Heterotypische Metaphase. × 2300. — *4*: *Ricinus communis*. Heterotypische Anaphase. × 4600. — *5*: *Neurada procumbens*. Heterotypische Metaphase. × 2300. — *6*: *Neurada procumbens*. Homotypische Metaphase. × 2300. — *7*: *Polygala triflora*. Heterotypische Metaphase. × 2300. — *8*: *Capparis Rothii*. Heterotypische Metaphase. × 2300. — *9*: *Euphorbia granulata*. Heterotypische Metaphase. × 2300. — *10*: *Euphorbia granulata*. Homotypische Metaphase. × 2300. — *11*: *Euphorbia scordifolia*. Homotypische Metaphase. × 2300.

liegendes Kraut sehr trockner Orte, das dem heissen Sand dicht angepresst ist. Zum Vergleich zeigt Fig. 11 eine systematisch nahestehende Art, *E. scordifolia* JACQ. (n = 10), die ebenfalls stark xerophil ist. Die zwei Arten wachsen oft vergesellschaftet und können einander in gewissen Formen sehr ähnlich sein. Fig. 9, 10 und 11 sind bei gleicher Vergrösserung gezeichnet, und man ersieht, dass die Pollenmutterzellen bei *E. granulata* am grössten sind, obgleich diese die kleinste Art darstellt. Die Chromosomen liegen deutlich zu zweien, und es liegt nahe, *E. granulata* als eine tetraploide Form einer mit *E. scordifolia* nahe verwandten Art aufzufassen. Bei andern *Euphorbia*-Arten hat HARRISON (in TISCHLER 1931) n = 10 und 20 vorgefunden. (Fig. 9—10; n = 2 × 10).

Cocculus leaeba DC. (Menispermaceæ). Eine hochwachsende Liane, die in der Sahara einheimisch ist. Die Chromosomen klumpen sich stark zusammen, und es ist schwierig, sie zu zählen, obgleich sie sehr gross sind. Nur wenige Arten dieser Familie sind zytologisch untersucht worden; LINDSAY (1930) hat jedoch bei *Menispermum canadense* n = 26 festgestellt. (Fig. 12; n = 13).

Crotalaria arenaria BENTH. (Papilionaceæ). Ein mehrjähriger Zwergstrauch, der an den trockensten Orten wachsen kann. Zum Vergleich habe ich am Niger *Crotalaria obovata* G. DON. eingesammelt, ein kräftiges Unkraut mittelfeuchter Orte; auch hier war n = 8 (Fig. 14). Dies sind die einzigen Arten der Gattung, deren Chromosomenzahlen bekannt sind; doch ist 8 eine gewöhnliche Zahl innerhalb der Leguminosen. (Fig. 13; n = 8).

Oldenlandia senegalensis HIERN. (Rubiaceæ). Ein hohes, schönes Kraut, das zwischen Gras an mittelfeuchten Orten wächst. Auf Schlamm wächst (periodischer Austrocknung ausgesetzt) die zarte *O. capensis* L., die 18 Chromosomen besitzt, die sehr deutlich gepaart sind und sogar in der heterotypischen Anaphase beisammen bleiben (Fig. 16). Die beiden Arten sehen sehr verschieden aus, sodass man beim ersten Anblick sich weigern möchte zu glauben, dass sie derselben Gattung angehören sollten. *O. capensis* scheint eine tetraploide Form zu sein, doch kaum von *O. senegalensis*. (Fig. 15; n = 9).

Trianthema crystallina V. (Aizoaceæ). Die drei untersuchten Arten der Gattung sind alle Sukkulenten. *T. polysperma* HOCHST. (Fig. 20), eine kleine einjährige Pflanze feuchten Bodens, besitzt ein von den beiden anderen Arten abweichendes Aussehen. Dagegen ähneln *T. pentandra* L. (Fig. 19) und *T. crystallina* V. (Fig. 18) einander aufs höchste, sowohl im Standort (trockner Sand) als auch im Aussehen. *T. pentan-*

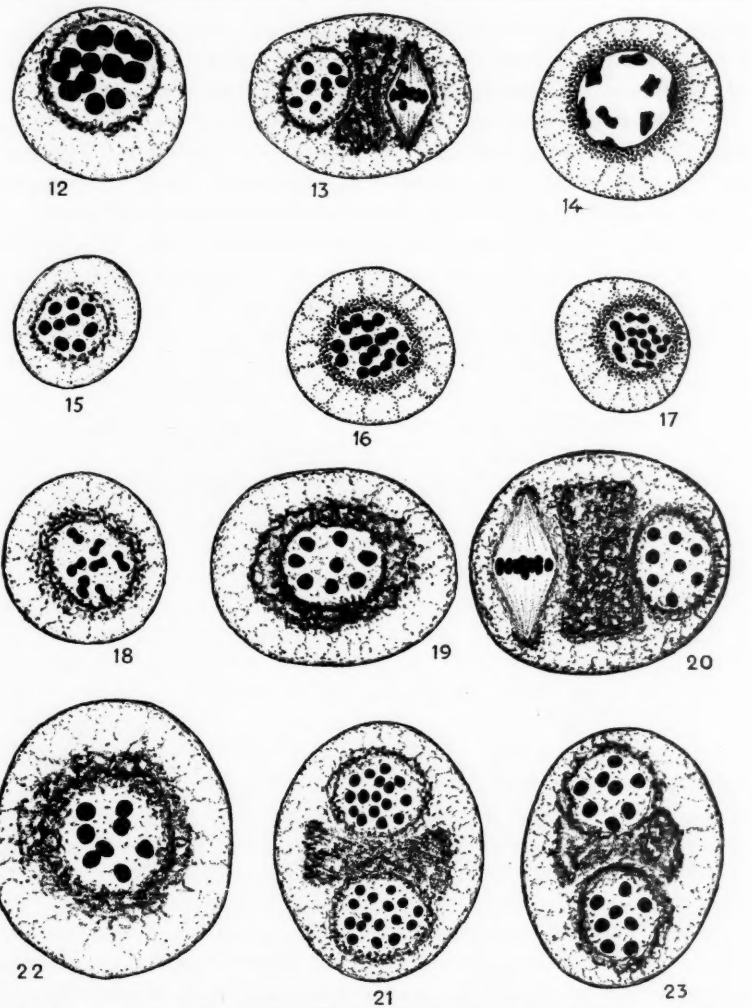


Fig. 12—23. — *12*: ***Cocculus leaeba.*** Heterotypische Metaphase. × 2300. — *13*: ***Crotalaria arenaria.*** Homotypische Metaphase. × 2300. — *14*: ***Crotalaria obovata.*** Diakinese. × 2300. — *15*: ***Oldenlandia senegalensis.*** Heterotypische Metaphase. × 2300. — *16*: ***Oldenlandia capensis.*** Heterotypische Metaphase. × 2300. — *17*: ***Oldenlandia capensis.*** Heterotypische Anaphase. × 2300. — *18*: ***Trianthema crystallina.*** Heterotypische Metaphase. × 2300. — *19*: ***Trianthema pentandra.*** Heterotypische Metaphase. × 2300. — *20*: ***Trianthema polysperma.*** Homotypische Metaphase. × 2300. — *21*: ***Indigofera sessiliflora.*** Homotypische Metaphase. × 2300. — *22*: ***Indigofera diphylla.*** Heterotypische Metaphase. × 2300. — *23*: ***Indigofera viscosa.*** Homotypische Metaphase. × 2300.

dra besitzt n = 8, während die weit kleinere *T. crystallina* (7 × 2 oder) 8 × 2 Chromosomen führt, die sehr deutlich paarweise angeordnet sind, als sei die Art tetraploid. (Fig. 18; n = 7 × 2 oder 8 × 2).

Indigofera sessiliflora DC. (Papilionaceæ). Dieser kleine Halbstrauch ist ein echter Xerophyt, dessen Sprosse auf dem gewaltig erhitzten Wüstensand niederliegen. Dasselbe gilt für die verwandte *I. diphylla*, die jedoch nur die halbe Chromosomenzahl besitzt (n = 8, Fig. 22). *I. viscosa* LAM. (Fig. 23) und *I. aspera* PERR. (Fig. 24) be-

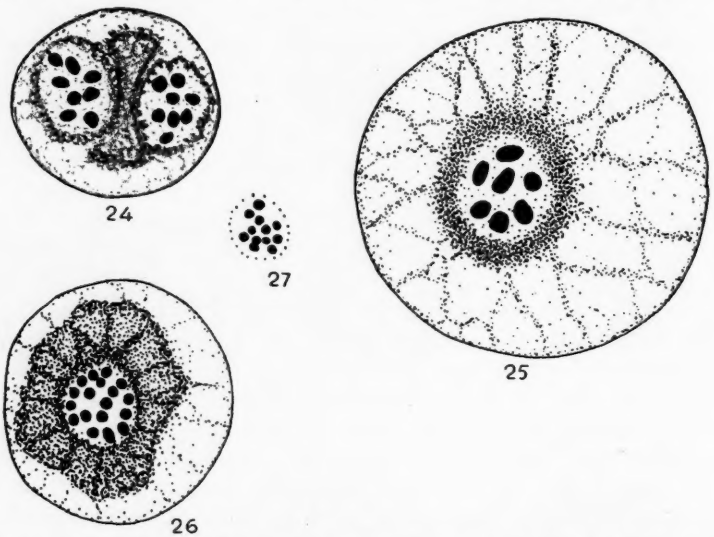


Fig. 24—27. — 24: *Indigofera aspera.* Homotypische Metaphase. × 2300. — 25: *Indigofera parviflora.* Heterotypische Metaphase. × 2300. — 26: *Bergia suffruticosa.* Heterotypische Metaphase. × 2300. — 27: *Bergia ammanoides.* Homotypische Anaphase. × 2300.

wohnen mittelfeuchte Orte der Savanne; auch bei ihnen ist n = 8, obgleich beide einer andern Sektion der Gattung angehören. *I. parviflora* HEYNE ist einjährig; sie besitzt grosse Pollenmutterzellen und Chromosomen, aber n = 7. Bei zwei anderen *Indigofera*-Arten ist n = 24 (KREUTER 1929, TSCHECHOWA 1930). (Fig. 21; n = 16).

Bergia suffruticosa FENZL. (Elatinaceæ). Bekanntlich sind die Elatinaceen meistens kleine, zarte Kräuter feuchter Orte. Ein solcher Typus findet sich auch auf Schlamm bei Timbuktu, nämlich die einjährige *Bergia ammanoides* ROTH. (Fig. 27); sie besitzt sehr kleine Kerne und Chromosomen; die Chromosomenzahl ist n = 12. Derselben

Gattung gehört ein ganz abweichender Typus an, nämlich *Bergia suffruticosa*, eine heidekrautartige Wüstenpflanze, die an *Empetrum* erinnert. Mit Spannung untersuchte ich sie und stellte n = 18 fest. Die Art hat eine sehr isolierte Stellung innerhalb der Gattung, und es lässt sich schwerlich entscheiden, ob sie triploid ist. Bei zwei *Elatine*-Arten fand FRISENDAHL (1927) »ca. 20 Chromosomen». (Fig. 26; n = 18).

Portulacca oleracea L. (Portulaccaceæ). Wie Fig. 28 zeigt, kommt *Portulacca* in zwei Formen vor, die so verschieden sind, dass man schon in einem Abstande von einigen Metern erkennen kann, welche man vor sich hat. Die eine ist schmächtiger, hat schmale Blätter und kleine Blüten. Die andere ist robust, besitzt doppelt so grosse und breite, keilförmige Blätter. Vom systematischen Gesichtspunkte aus könnte man sehr wohl die eine als Varietät der andern aufstellen; doch sieht man gleich, dass sie sehr nahe verwandt sind, da die Verschiedenheiten wesentlich nur Grössenunterschiede darstellen. Sie wachsen untereinander; leider habe ich zu wenig Herbarmaterial zur Verfügung gehabt und kann daher nicht entscheiden, ob es die grosse Form ist, die am weitesten in die Sahara eindringt.

Die kleine Form hat n = 9 (Fig. 29) gleichwie *Portulacca grandiflora* (TJEBBES 1930). Bei der grossen Form (var. *gigas*) dagegen ist n = 27 (Fig. 30), und da sich keine anderen, ähnlichen Arten in der Nähe befinden, liegt kaum ein Grund vor daran zu zweifeln, *dass die grössere Form ein Hexaploid der kleineren darstellt.* (Fig. 28—30; n = 9 und 9 × 3).

Aerva tomentosa FORSK. (Amaranthaceæ). Wie Fig. 30 A zeigt, verhält *Aerva* sich auf ähnliche Weise wie *Portulacca*, indem es sowohl eine zarte, schmalblättrige (= var. *Bovei* WEBB.), als auch eine kräftige, breitblättrige Form gibt, die bei Timbuktu oft nebeneinander wachsen. Es ist die breitblättrige Form, die in den *milderen* Klimas gegen Süden vorkommt, während die schmalblättrige das Klima weit in die Sahara hinein erträgt (K. GRAM). *Die beiden Typen besitzen also verschiedene Dürreresistenz,* was in ihrer *abweichenden geographischen Ausbreitung* zum Ausdruck kommt. Leider kann ich nicht angeben, welche von den beiden Formen die Gigas-Form ist, da seltsamerweise sämtliche Individuen bei Timbuktu weiblich sind; sie müssen sich also parthenogenetisch vermehren. Die Art vermehrt sich ausschliesslich durch Samen, und Keimpflanzen sind sehr häufig. Es war mir nicht möglich die Chromosomen in den vegetativen Mitosen zu zählen. (Fig. 30 A).

Eragrostis cambessediana KUNTH (Gramineæ). Zu den interessan-

testen der untersuchten Typen gehören jedenfalls einige Formen, die sich in systematischer Hinsicht um *Eragrostis cambessediana* KUNTH (Fig. 31 *A*) gruppieren, einem schönen Gräschen, dass den Schlamm der Seeufer bewohnt, solange diese nicht unter Wasser stehen. Diese zarte Pflanze fordert die bestmöglichen Standortsbedingungen, um leben zu können, nämlich eine stets feuchte Erde und ausserdem eine

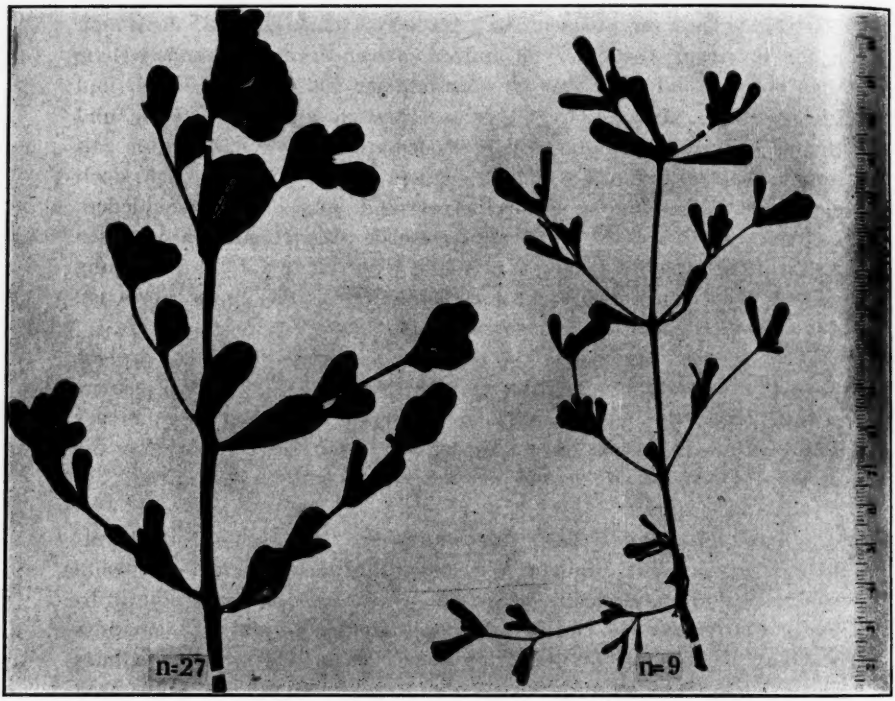


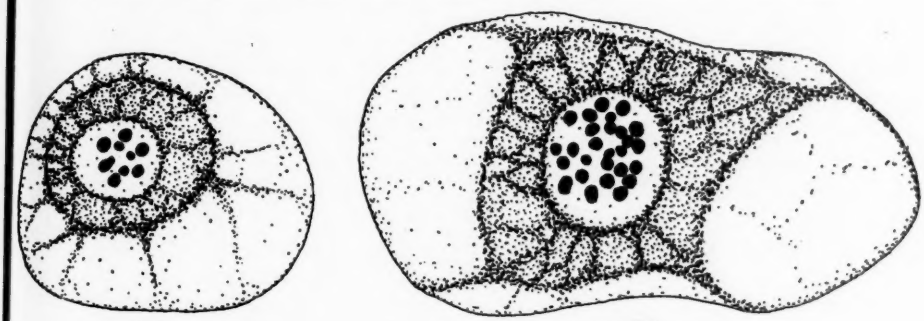
Fig. 28. *Portulacca oleracea.* Die zwei Formen: n = 9 und n = 3 × 9.

stets dampfgesättigte Luft sehr hoher Temperatur (ca. 40°). Zu Beginn der Überschwemmungen wird die Pflanze getötet, sie ist also nur einjährig. Ihre Chromosomenzahl beträgt nur 10. (Fig. 32).

Ganz nahe der kleinen Seen, an deren Ufer *E. cambessediana* wächst, liegen die sehr trocknen Dünen, die eine ausgeprägt xerophile Flora beherbergen. Am Fuss der Dünen, wo die Überschwemmungen nicht hinaufreichen, gibt es mittelfeuchte Orte mit ihren speziellen Arten, die weder Hygrophyten noch Xerophyten sind. Hier findet sich

auch eine *Eragrostis albida* HITCH. die *E. cambessediana* aufs höchste ähnelt. Sie ist häufig etwas kleiner (Fig. 31 *B*) und mit borstenförmigen Blättern versehen, weicht jedoch besonders dadurch ab, dass sie mehrjährig ist. Sie ist also im Stande das ganze Jahr hindurch zu arbeiten, da sie nicht so grosse Ansprüche an Luft und Bodenfeuchtigkeit hat, und daher ein weniger günstiges Terrain zu bewohnen vermag als die anspruchsvolle *E. cambessediana*, dessen tetraploide Form sie offenbar darstellt. (Fig. 33).

Steigen wir nun etwas höher hinauf auf die Düne, gelangen wir zu Lokalitäten, die noch viel trockner sind, indem nicht nur die Luft, sondern auch die Erde bis auf 80° erwärmt wird. Hier können die beiden erwähnten Arten nicht wachsen; jedoch treffen wir nun eine



29 30

Fig. 29. *Portulacca oleracea.* Homotypische Metaphase (n = 9). × 2300.
Fig. 30. *Portulacca oleracea* var. *gigas.* Heterotypische Metaphase (n = 27). × 2300.

Eragrostis pallescens HITCH. Sie ähnelt auch den beiden vorigen Arten (Fig. 31 *C*), weicht jedoch besonders dadurch ab, dass sie ebenso kräftig ist, wie unsre einheimische *Dactylis*; sie besitzt recht breite Blätter, die sich jedoch einrollen können. Die Art ist mehrjährig und steht auch in der langen, intensiven Trockenzeit mit lebendigen Blättern, besitzt also eine sehr grosse Dürreresistenz; ihre Chromosomenzahl ist 40. (Fig. 34).

Als ich die Pflanzen einsammelte, konnte ich keine anderen Verschiedenheiten erkennen, als Grössen- und Standortsunterschiede, weshalb ich sie für polyploide Formen derselben Art hielt. Um jedoch eine objektive Beurteilung der Frage zu erhalten, habe ich die Pflanzen dem bekannten Gras-Spezialisten Dr. A. S. HITCHCOCK zugesandt, der die beiden Formen als neue Arten beschrieben hat. Es hat in dieser Verbindung jedoch keine entscheidende Bedeutung, welchen systematischen Wert man den beiden neuen Formen beimisst.

Bei anderen *Eragrostis*-Arten stellte AVDULOW (1931) die Zahlen 10, 20 und 30 fest.

III. ZUSAMMENFASSENDE BETRACHTUNGEN.

Im vorhergehenden Abschnitt wurde das Resultat einer zytologischen Untersuchung folgender 29 Pflanzenarten aus der Umgebung von Timbuktu in der südlichen Sahara mitgeteilt:

	n =
Cucumis prophetarum	12
Launaea integrifolia	8
Farsetia ramosissima	12
Ricinus communis	10
Neurada procumbens	7
Polygala triflora	19
Capparis Rothii	2×10
Euphorbia granulata	2×10
» *scordifolia*	10
Cocculus leaeba	13
Crotalaria arenaria	8
» *obovata*	8
Oldenlandia senegalensis	9
» *capensis*	2×9
Trianthema crystallina	2×8 (oder 2×7)
» *polysperma*	8
» *pentandra*	8
Indigofera sessiliflora	2×8
» *diphylla*	8
» *parviflora*	8
» *viscosa*	8
» *aspera*	8
Bergia suffruticosa	18
» *ammanoides*	12
Portulacca oleracea	9
» » var. *gigas*	3×9
Eragrostis cambessediana	10
» *albida*	20
» *pallescens*	40

Die Auswahl der Arten ist recht beliebig; doch habe ich namentlich solche Typen untersucht, die mit nahe verwandten Formen von womöglich gleicher Gattung und aus derselben Gegend verglichen wer-

Fig. 30 A. *Aerva tomentosa*; die zwei Formen.

den konnten. Ausserdem habe ich die etwas mangelhafte Methode benutzt, die darin besteht, zu untersuchen, ob die Chromosomen paarweise angeordnet liegen. Auf diese Weise ist es — mit einem grösseren oder geringeren Grad von Sicherheit — gelungen, bei mehr als der Hälfte der untersuchten 17 Gattungen eine Polyploidie nachzuweisen; am deutlichsten war diese in den Gattungen *Portulacca* (Fig. 28) und *Eragrostis* (Fig. 31).

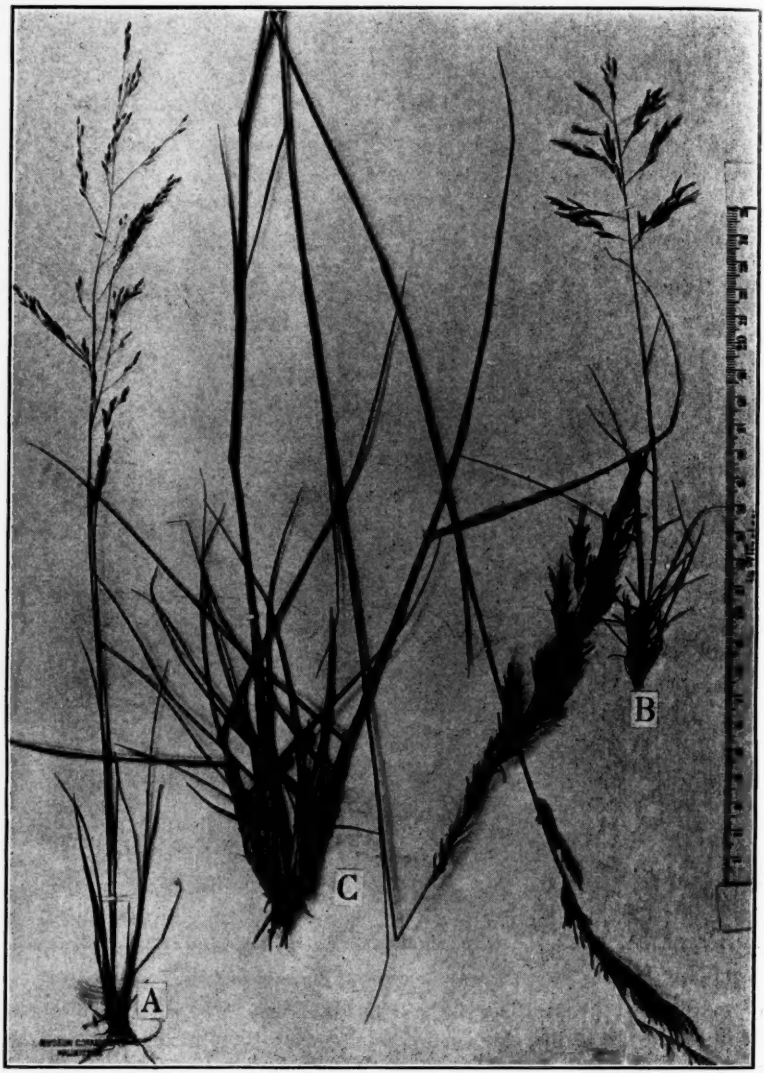


Fig. 31. *Eragrostis.* A: *E. cambessediana* (n = 10); B: *E. albida* (n = 20); C: *E. pallescens* (n = 40).

Ausserdem fand ich, dass noch folgende Arten in zwei Formen, einer grösseren und einer kleineren, auftraten: *Aerva tomentosa* FORSK. (Fig. 30 A) (Amaranthaceæ), *Glinus lotoides* LOEFL. (Aizoaceæ) und *Polycarpon Loeflingii* BENTH. & HOOK. (Caryophyllaceæ); jedoch habe ich bei diesen Arten die bezüglichen Chromosomenzahlen nicht feststellen können.

Die gefundenen polyploiden Typen weichen von den entsprechenden diploiden Arten ab: 1) *Morphologisch*; 2) *Ökologisch* und *pflanzengeographisch* (Lebensform); 3) *Genetisch*.

In morphologischer Hinsicht weichen die Formen mit den höheren Chromosomenzahlen (die »Polyploiden») namentlich durch Grössenunterschiede ab. Meistens ist die polyploide Form die *grösste*, z. B.

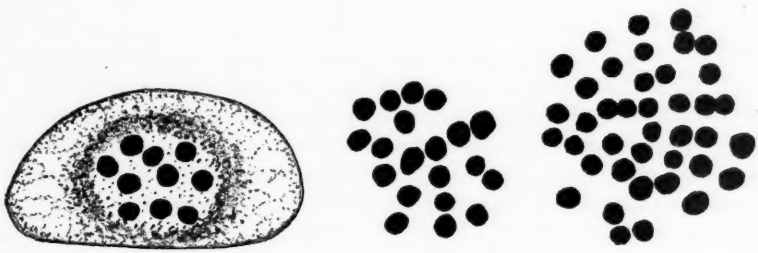


Fig. 32. *Eragrostis cambessediana.* Heterotypische Metaphase. × 4600. n = 10.
Fig. 33. *Eragrostis albida.* Heterotypische Metaphase. × 4600. n = 20.
Fig. 34. *Eragrostis pallescens.* Heterotypische Metaphase. × 4600. n = 40.

Portulacca und *Eragrostis*, und verdient also die Bezeichnung »Gigas». Seltener findet man die hohen Chromosomenzahlen bei relativ *kleinen* Arten, z. B. bei *Oldenlandia capensis*, *Trianthema*; und in der Arktis ist *Kalmia glauca* (n = 24) viel kleiner als *K. latifolia* (n = 12).

Besonders interessant ist aber, dass mit *dem erhöhten Chromosomenbestand auch eine gesteigerte »Vitalität»* (vegetative Kraft) *folgen kann*, so dass *die Pflanze eine grössere Widerstandsfähigkeit gegen Austrocknung besitzt*. Hieraus kann wieder resultieren, dass *die polyploide Pflanze nun die ganze furchtbare Trockenzeit überleben kann*, so dass sie also *ihre Lebensform gewechselt hat*. So ist z. B. *Eragrostis cambessediana* (n = 10) Therophyt, während sowohl *E. albida* (n = 20) als auch *E. pallescens* (n = 40) Hemikryptophyten (RAUNKIÆR) sind.

Wir sahen schon, dass gewisse Polyploiden (z. B. *Eragrostis*) auf einem Boden wachsen können, der der diploiden Form schon zu un-

günstig ist. Mit andern Worten: *die geographischen Grenzen der Art verschieben sich, wenn Polyploidie eintritt.*

Die Art kann durch Polyploidie ihre Ausbreitung verändern, nicht nur bezüglich ihrer Standortsverhältnisse, sondern auch in geographischer Hinsicht (*Aerva*). Falls diese Hypothese, die bisher nur auf ganz wenige Beobachtungen fusst, sich als stichhaltig erweisen würde, könnte man annehmen, in den günstigen Klimaten der Erde (z. B. im tropischen Regenwald) verhältnismässig viel niedrige, dagegen z. B. in Wüsten und arktischen Gebieten höhere Zahlen zu finden.

Auch bei anderen Pflanzen kennt man ähnliche Erscheinungen; namentlich sind TURESSONS (1930) Untersuchungen über *Festuca ovina* interessant: Mit zunehmender Polyploidie wurden die Pflanzen vegetativ kräftiger, während die Fertilität abnahm (Viviparie).

Endlich sei noch erwähnt, dass *die Polyploiden neue genetische Möglichkeiten enthalten können.* Dass *die Polyploidie erblich sein kann*, zeigt z. B. *Empetrum hermaphroditum*, das oft in den nördlichsten Gegenden der Erde vorherrscht, wo die diploide Form (*E. nigrum*) gar nicht leben kann. Rein theoretisch gibt es viele neue Kombinationsmöglichkeiten; man denke sich z. B. eine tetraploide Form mit einer diploiden derselben oder einer nahestehenden Art gekreuzt. Bei *Bicornes* findet sich, wie schon erwähnt, eine schöne 6-Reihe; unter diesen Zahlen kommt indessen auch die Zahl 23 (*Pyrola*) vor, die wohl sicher von der Zahl $24 = 2 \times 12$ abzuleiten ist. Eine Phase der phylogenetischen Entwicklung, die *Pyrola* durchlaufen hat und die zur Zahl 23 geführt hat, würde dann schematisch als $(2 \times 12) \div 1$ zu schreiben sein. Die Polyploidie kann also bei der weiteren phylogenetischen Entwicklung beibehalten werden. Vielleicht stirbt auch die tetraploide Form aus, weil sie die schwächere ist, und wir erhalten die multiplen Chromosomenreihen, die für viele systematische Einheiten so charakteristisch sind.

Tiefergehende Untersuchungen müssen entscheiden, welche Rolle die Polyploidie bei den Prozessen, die zur *Artbildung* führen, spielt; dass den Polyploiden jedoch eine grosse Rolle zukommt, davon zeugen offenbar die häufigen Reihen multipler Chromosomenzahlen. »Il est raisonnable d'admettre que la polyploidie est un facteur qui peut avoir son influence dans l'évolution du genre» (FERNANDES 1931, p. 107).

Bezüglich der Frage, wie Polyploidie *entstehen* kann, wissen wir, dass diese sowohl in vegetativen Zellen, als auch nach Bastardierung zustande kommen kann (ROSENBERG, MÜNTZING). In diesem Zusammenhang ist es nun besonders interessant, dass *Polyploidie durch direkte*

Einwirkung äusserer Faktoren (sowohl auf Soma als auch auf junge Geschlechtszellen) *herbeigeführt werden kann.* Durch *Wundreiz* brachte DE MOL polyploide holländische Blumenzwiebeln hervor, und auf ähnliche Weise entstanden JÖRGENSEN's polyploide Solanaceen. Auch Geschlechtszellen können durch Einfluss verschiedener äusserer Faktoren polyploid werden, eine Erscheinung, die in jüngster Zeit von einer Reihe von Forschern untersucht worden ist. Man hat sich dabei der verschiedensten Einwirkungsmethoden und Pflanzen bedient: GOODSPEED (1930) hat Röntgenstrahlen angewandt, HEILBRONN (1928) arbeitete mit Farnen, MICHAELIS (1928) mit *Oenothera* und *Epilobium.* Am besten untersucht sind indessen die durch Temperaturveränderungen hervorgerufenen Wirkungen. Schon 1922 machte BORGENSTAM einleitende Versuche. Viele andere Forscher sind ihm später nachgefolgt: SAKAMURA und STOW (1926), SHIMOTOMAI (1927), STOW (1930), HEILBORN (1928—30) und manche andere könnten noch genannt werden; da aber die wichtigsten Arbeiten bei HEILBORN (1930) ausführlich referiert sind, begnüge ich mich hier mit einem Hinweis auf diese Arbeit. Als Hauptresultat geht aus den erwähnten Untersuchungen hervor, dass *durch Einfluss extremer, sowohl hoher als niedriger Temperaturen, Geschlechtszellen mit abweichenden, oft gerade polyploiden Chromosomenzahlen entstehen können.*

Polyploiden können also durch starke äussere Einwirkungen entstehen. In der *Kultur* werden den Pflanzen oft solche ihnen unnatürliche äussere Bedingungen geboten. Man kreuzt sie z. B.; die grössten polyploiden Exemplare werden dann als die ertragreichsten aussortiert. Übereinstimmenderweise wurden die ersten Polyploiden bei angebauten Pflanzen entdeckt. Der erste wildwachsende Polyploid wurde von PACE 1914 gefunden, der nächste von JÖRGENSEN (1923) und in den Jahren 1927—30 sind mehrere neue Fälle wildwachsender Polyploiden veröffentlicht worden (z. B. *Viola*). Eine vollständige Liste derselben gibt CLAUSEN (1931). In den nächsten Jahren wird sich wohl erweisen, dass *Polyploidie auch in der freien Natur eine recht allgemeine Erscheinung ist.*

Will man nach der Ursache des Entstehens der Polyploiden in der Natur fragen, so liegt es nahe darauf hinzuweisen, dass *solche extreme äussere Bedingungen, die in den Laboratorien Polyploidie herbeiführen können, auch in der Natur vorkommen.* Im Jahre 1924 beobachtete ich z. B., dass *Empetrum* in Nord-Grönland zur Zeit der Reduktionsteilung in der Nacht einer Kälte von mehr als $\div 5°$ ausgesetzt worden ist. Am frühen Morgen waren die Blütenknospen von einer dicken

Eiskapsel umgeben und waren Druck und Abkühlung ausgesetzt; dann kommt plötzlich die Wärme; die Pflanze wächst weiter und die Reduktionsteilung wird fortgesetzt.

Nicht nur die niedrigen Temperaturen der Laboratorien, auch die hohen findet man in der Natur wieder. In der südlichen Sahara musste ich dicksohliges Winterfusszeug anhaben, wenn ich zwischen den Sandpflanzen gehen wollte ohne die Füsse zu verbrennen. Der Sand ist nämlich an den meisten Tagen des Jahres auf 70—80° C erhitzt, also eine Temperatur, die man im Laboratorium als über »die kritische Temperatur» liegend erachten würde, und die weit höher ist als die Temperaturen, die bei den Laboratoriumversuche die Entstehung von Polyploiden verursachen. Aber bei diesen für den Menschen so kritischen Temperaturen führen die Pflanzen Reduktionsteilungen aus; meine Fixierungen zeigen, dass die Pflanzen selbst in den wärmsten Augenblicken der heissesten Tage in Reduktionsteilung stehen, selbst an den am stärksten erhitzten Orten, wo ein Mensch nur kurze Zeit zu leben vermag. Die Teilungen finden hier zu *allen Tageszeiten* statt; doch sind die Chromosomen, wenn es am wärmsten ist, dicht zusammengeklumpt, so dass man sie bei *Boerhaavia repens* z. B. nicht zählen kann.

Wir müssen also damit rechnen, dass *es nicht nur in den Laboratorien solche Temperaturen gibt, die Polyploide hervorbringen können; die Natur macht dieselben »Versuche» mit demselben Resultate* wie oben beschrieben.

Und wie der Gärtner sich die lebensfähigsten Individuen zur Zucht herauswählt, so erfolgt z. B. bei Timbuktu ebenfalls die interessanteste »natural selection» in folgender Weise. Nach Verlauf einer ca. $^3/_4$ jährigen furchtbaren Trockenzeit wird die Regenzeit von entsetzlichen Sandstürmen eingeleitet, die den Wüstensand mit den darin enthaltenen Samen fast sämtlicher Arten hoch über die Hausdächer emporheben. Am Morgen nach einem solchen Sturm sieht man die Negersoldaten oben auf dem flachen Tondach der Festung die hier hinauftransportierte Masse in grossen Mengen hinunterschaufeln. Wie effektiv diese Samenverbreitung ist enthüllt bald die Regenzeit, denn dann ist selbst der grosse Turm der stattlichen Moschee ganz bis an die Spitze mit Keimpflanzen von *Portulacca*, *Tribulus*, *Boerhaavia* usw. bedeckt, dessen Samen der Wind dahin gebracht hat. Wenige Tage später ist die öde Wüstenlandschaft umgewandelt, und mit einem Grün von der Üppigkeit eines tropischen Regenwaldes bekleidet; und der Wettlauf um die Samenreife geschieht in der gewaltigen Wärme und Feuchtigkeit mit fieberhafter Geschwindigkeit.

Nach Verlauf eines Monats fängt der Regen an abzunehmen, und dann kommt der Wettlauf mit dem Tode, vielleicht die interessanteste Phase des ganzen »Abenteuers». Zuerst sterben die Hygrophyten, die der Wind auf den Dünen ausgesät hat; dann folgen die Mesophyten im Wüstensand usw. *Alle Arten stehen jetzt mit Blütenknospen in der Reduktionsteilung, und jetzt ist die Dürre und Wärme derart, dass Polyploide in der Natur wie im Laboratorium entstehen können. Die Samen aller Arten sind vom Wind an sämtlichen Orten ausgesät, und nun bewirkt das Klima die Auslese der wenigen Arten, die auf den verschiedenen Lokalitäten »the fittest» sind.* Wurden z. B. die drei *Eragrostis*-Arten auf den Gipfeln der Dünen ausgesät, stirbt zuerst die Form mit $n = 10$ (*E. cambessediana*), dann die mit $n = 20$ (*E. albida*), und nur die mit $n = 40$ (*E. pallescens*) bleibt übrig.

In dieser Arbeit ist namentlich der Einfluss der *Temperatur* (und dem davon abhängigen *Feuchtigkeitsgrad*) auf das Entstehen der Polyploidie berücksichtigt worden. Die nächste Aufgabe wäre dann die Bedeutung auch derjenigen anderen Verhältnisse zu untersuchen, die das Leben der Pflanze draussen in der Natur bedingen. Die ganz wenigen Laboratoriumversuche, die vorliegen, lassen vermuten, dass wenn z. B. Austrocknung, gewisse Lichtstrahlen, Wundreiz usw. Polyploidie herbeiführen können, dann vielleicht auch andere Verhältnisse (z. B. Wasserstoffionenkonzentration), die das Gedeihen der Pflanzen in der Natur bedrohen, die Chromosomenzahlen der Pflanzen ändern könnten. *Dadurch würden neue Typen entstehen, die einen andern ökologischen, pflanzengeographischen und genetischen Wert besässen.* Dabei brauchten nicht nur solche Typen zu entstehen, die grössere Dürre ertragen, sondern vielleicht gerade solche, die mehr Feuchtigkeit ertragen könnten. So war der kleine Hygrophyt *Oldenlandia capensis* tetraploid, im Gegensatz zu *O. senegalensis*, der auf einem trockneren Boden wächst, wie auch die meisten anderen Arten der grossen Gattung. *Natürlich darf man nicht annehmen, dass ausschliesslich in den kältesten und wärmsten Gegenden der Erde Polyploide zu finden sind; solche gibt es vermutlich in allen Gegenden der Erde, wo die Pflanzen ihnen feindlichen äusseren Einwirkungen ausgesetzt sind.*

Die durch Polyploidie entstandene »Anpassung» ist demnach nicht langsam und kontinuierlich entstanden (LAMARCK), sondern gerade stossweise wie eine Mutation.

Eine befriedigende Beantwortung aller dieser Fragen muss der Zukunft vorbehalten werden. Die schon vorliegenden wenigen Beobachtungen lassen jedoch vermuten, dass wir *durch Studien über Poly-*

ploidie das Problem der Anpassung und der Phylogenie der Pflanzen — ausgehend von der Einwirkung äusserer Faktoren — in neuem Licht sehen werden.

Bei Hinblick auf diese allgemeinen Zusammenhänge zwischen zytologischen und pflanzengeographischen Problemen erkennt man schon jetzt die Linien einer künftigen Arbeitsgemeinschaft einiger Hauptzweige der botanischen Wissenschaften, die einander bisher ferne standen.

IV. ZUSAMMENFASSUNG.

1. In vorliegender Arbeit (S. 30) werden die *Chromosomenzahlen* (n) von 29 Pflanzen der südlichen *Sahara* mitgeteilt.

2. Ein Teil der untersuchten Pflanzen sind *Polyploide*, die im Vergleich mit ihren Stammarten neue a) *genetische* und b) *morphologische* Eigenschaften erworben haben, wodurch sie befähigt wurden an anderen Orten zu wachsen, sodass sie sowohl einen neuen c) *ökologischen* als auch d) *pflanzengeographischen Wert besitzen können.*

3. Laboratoriumversuche anderer Forscher haben erwiesen, dass Polyploide durch Einfluss ungünstiger äusserer Einwirkungen (Wärme, Kälte usw.) entstehen können. Da die Pflanzen in der Natur (z. B. Sahara) ähnlichen extremen Umweltbedingungen ausgesetzt sind wie die bei den Laboratoriumversuchen verwandten, darf man annehmen, dass *Polyploide auch in der Natur infolge ungünstiger äusserer Einwirkungen entstehen.*

4. Die Konsequenzen hiervon sind, *dass die äusseren Faktoren, indem sie Polyploide hervorbringen, anscheinend bei den artbildenden Prozessen stark mitwirken,* (Ausführliches findet man S. 30—37), *und dadurch wohl das Entstehen neuer Arten veranlassen können.*

Das Carlsbergfond in Kopenhagen hat mehrere Jahre hindurch sowohl meine Studienreisen als auch die Bearbeitung des eingesammelten Materials unterstützt; ich erlaube mir hiermit, der Direktion des Fonds meinen aufrichtigen Dank auszusprechen.

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ZYTOLOGISCHE UND EXPERIMENTELLE STUDIEN IN DER GATTUNG TARAXACUM

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(With a summary in English)

EINLEITUNG.

WÄHREND der grossartigen Entwicklung der experimentellen Botanik und Pflanzenembryologie im Anfange dieses Jahrhunderts wurde die Aufmerksamkeit durch eine Reihe von Untersuchungen vor allem von JUEL, MURBECK, OSTENFELD, STRASBURGER und ROSENBERG auf das häufige Vorkommen ohne Befruchtung entwickelter diploider Embryonen innerhalb der Pflanzengattungen gelenkt. Besonders bei den Arten und Artengruppen der polymorphen Pflanzengattungen *Rosa*, *Rubus*, *Taraxacum* und *Hieracium*, die seit altem als schwer klarzulegend betrachtet wurden, trugen diese Entdeckungen zur Erklärung der Verbreitung und relativen Konstanz der zahlreichen ohne Zweifel hybridogenen Formen bei. In dieser letzten Hinsicht grundlegend waren die Kreuzungen LIDFORSS' (1907, 1914) zwischen *Rubus plicatus* und *cæsius* (sowie auch *tomentosus* × *vestitus*, *polyanthemus* × *Bellardii* etc.), wobei die vielförmige Nachkommenschaft in F_1 unzweideutig zeigte, dass die benutzten Eltern stark heterozygot waren, und dasselbe ging auch aus OSTENFELDs Kreuzungsexperimenten (1910) in der *Hieracium Pilosella*-Gruppe, z. B. zwischen *H. auricula* und *aurantiacum*, hervor.

Etliche neue Probleme entstanden aber und es waren vor allem zwei, die früh in den Brennpunkt des Interesses traten: die Ursachen für die Entstehung der apomiktischen Fortpflanzungsweise, ob eine unmittelbare Folge der postulierten Hybridisierung (ERNST 1918) oder nur eine Erscheinung, von dieser unabhängig und von inneren genetischen Faktoren bedingt (WINKLER 1920), und die Wege, auf denen die Neubildung der zahlreichen Biotypen in den fraglichen Gattungen erfolgt ist, ob durch sexuelle Spaltungs- und Wiederkreuzungsprodukte oder auf vegetativem Weg durch sprungweise Veränderungen der Genmasse der Biotypen. Mit Ausnahme der klassischen Arbeiten von LIDFORSS und OSTENFELD sind nur wenige experimentelle Studien ausgeführt worden, und die zahlreichen zytologischen Untersuchungen

haben die Probleme nicht zu voller Klarheit bringen können. Als ich im Frühjahr 1930 die Gattung *Taraxacum* zur Behandlung aufnahm, schien es mir daher erforderlich sowohl experimentell durch Kastrations-, Kreuzungs- und Formenbildungsuntersuchungen als auf zytologischem und embryologischem Weg die Bedingungen für die Entstehungsweise und Fortpflanzungsverhältnisse eines der parthenogenetischen Formenkreise klarzulegen.

Die etwa 150 verschiedenen *Taraxacum*-Biotypen, die ich jetzt auf den Svalöfer Versuchsfeldern in Kultur habe, sind zum Teil auf Reisen in verschiedenen Gegenden Schwedens eingesammelt worden. Viele interessante Klonen habe ich auch von den Herren G. HAGLUND, Uppsala, T. BORGVALL, Gothenburg, E. SÖDERBERG, Stockholm, Professor C. SKOTTSBERG, Gothenburg, und vor allem durch den Herrn Akademiegärtner N. HAGMAN, Lund, bekommen. Sowohl diesen als auch Herrn Dozent A. HÅKANSSON, Lund, der mir mit Ratschlägen hinsichtlich der zytologischen Technik beigestanden hat, spreche ich meinen herzlichsten Dank aus.

KASTRATIONSVERSUCHE UND CHROMOSOMENZAHLEN.

Die skandinavische *Taraxacum*-Flora, deren Erforschung und Klarlegung wir vor allem den Arbeiten DAHLSTEDTS verdanken, wird am besten in sechs grosse Hauptgruppen eingeteilt: *Erythrosperma*, *Obliqua* (+ *Dissimilia*), *Palustria*, *Spectabilia*, *Ceratophora*, *Vulgaria* (+ die unten aufgestellten *T. maculigerum*-Gruppe). Die morphologischen, biologischen und zytologischen Charaktere dieser Gruppen berechtigen zu der Annahme, dass ihre Zusammensetzung und phylogenetische Abstammung im grossen gesehen verschieden, die Gruppen natürlich und nach der von TURESSON (1929) aufgestellten Terminologie als verschiedene Agamospezies zu betrachten sind.

Durch RAUNKIÆRS Untersuchungen (1903) wurde experimentell bewiesen, dass sämtliche von ihm untersuchte *Taraxacum*-Biotypen ohne Befruchtung Samen ausbilden. Untersucht wurden in *Erythrosperma T. decipiens* RAUNK. (bildet keinen Pollen), in *Spectabilia T. croceum* DT. (ohne Pollen), in *Palustria T. paludosum* SCOP. (= *T. balticum* DT.?; ohne Pollen), in *Vulgaria T. Ostenfeldii* RAUNK. (ohne Pollen), *T.* »*vulgare*» LAM. (Pollen), *T. Gelertii* RAUNK. (Pollen), *T. speciosum* RAUNK. (ohne Pollen) und ausserdem zwei Biotypen aus dem Südwesten Europas und aus Vorderasien ausserhalb der grossen apomiktischen Formenkreise *T. obovatum* DC. und *T. glaucanthum* DC. (nach HANDEL MAZZETTI mit *T. dissectum* LEDEB. identisch).

Durch diese Kastrationsversuche hielt sich RAUNKIÆR *berechtigt anzunehmen, dass überhaupt alle Taraxacum-Arten apomiktisch sind und die Parthenogenesis von Kreuzungen unabhängig entstanden ist, ehe noch die jetzigen Arten und Formen ausdifferentiert worden waren.* Wenn man bedenkt, dass nur in Schweden durch DAHLSTEDTs Beschreibungen 14 Arten innerhalb *Erythrosperma*, 4 innerhalb *Obliqua*, 4 innerhalb *Ceratophora*, 6 innerhalb *Palustria*, 14 innerhalb *Spectabilia* und 62 innerhalb *Vulgaria* bekannt sind, und dass die Gattung *Taraxacum* in eine ganze Reihe sehr verschiedener, ungleich alter Sektionen eingeteilt ist, scheint diese Annahme recht kühn zu sein. Auch zeigte ROSENBERG schon 1909 normale Reduktionsteilung bei einer von DAHLSTEDT kultivierten, zum *Vulgaria*-Komplex gehörigen unbeschriebenen Art, *T. confertum* (DAHLSTEDT 1920; extraskandinavisch?), das Auftreten von acht Doppelchromosomen und die Ausbildung einer Makrosporentetrade zum Unterschied der von MURBECK (1904) und JUEL (1905) untersuchten Biotypen, wo die Makrosporenmutterzelle nur eine Dyade und einen mit der diploiden Chromosomenzahl versehenen Embryosack bildet. 1910 und 1913 fanden IKENO und OSAWA noch eine sexuelle Art, *T. platycarpum* DT., am nächsten zum *Ceratophora*-Komplex gehörig (DAHLSTEDT 1907 a, S. 3), die sich durch diploide Chromosomenzahl, normale Reduktionsteilung und Makrosporentetrade auszeichnet.

Für ein tieferes Eindringen in die Entwicklungsgeschichte dieser Gattung schien es mir notwendig, Kastrationsexperimente in grossem Umfange auszuführen, und *schon im Herbst 1930 gelang es mir, noch eine sexuelle Art 1929: 4, aus Palermo unter dem Namen von T. minimum* (= *megalorrhizon* HAND. MAZZ.?) *erhalten, zu finden*, die auf Grund der Resultate zahlreicher Kastrationen (etwa 10 Blütenkörbe), der kleinen Chromosomenzahl und der normalen Teilungen der Pollenmutterzellen als sexuell betrachtet werden muss. Die unten angegebenen Kastrationen, die nach der von RAUNKIÆR und OSTENFELD beschriebenen Methode ausgeführt sind, sowie das Vorkommen der triploiden Chromosomenzahlen[1] in der Gattung berechtigen zu der Annahme, dass sexuelle Biotypen innerhalb der apomiktischen Formenkreise, insbesondere natürlich der triploiden Gruppen — wenn sie über-

[1] An und für sich berechtigen die triploiden Zahlen nicht zur Annahme von Apomixis. Vollständige Paarung der Chromosomen könnte ja durch Autosyndese hervorgebracht werden. Bisherige Untersuchungen der Reduktionsteilung, über die ich später berichten werde, haben gezeigt, dass Störungen der Meiosis, z. B. mangelhafte oder fehlende Paarung der Chromosomen, in hohem Grad vorkommen.

haupt vorkommen (*T. confertum* Dt.?) — äusserst selten sind; auch die untersuchten Tetraploiden, 1930: 128 und die *Spectabilia*-Formen, haben sich als apomiktisch erwiesen, und das Vorkommen fakultativer Sexualität unter diesen letzteren in dem Sinne, dass es neben den parthenogenetischen auch sexuelle Biotypen geben würde (Dahlstedt 1923), ist sehr unwahrscheinlich. Die zahlreichen negativen Kastrationen beruhen darauf, dass anfangs ein zu grosser Teil des Blütenkorbes weggeschnitten wurde; es genügt natürlich schon, die obersten Teile der Griffel zu entfernen. Die Pergamintüten wurden stets erst ein paar Tage nach dem Kastrieren aufgesetzt, sodass konstatiert werden konnte, dass die Narben immer mit weggenommen worden waren.

KASTRATIONSVERSUCHE.

	Erythrosperma.	Anz. kastr. Individuen	Positive Kastr.	Negative Kastr.
1929: 6:	Brünn, Botanischer Garten, unter dem Namen *T. lævigatum*	5	17	0
1930: 1:	Schweden, Malmö	4	9	0
1930: 2:	» »	1	2	0
1930: 6:	» Lund	3	6	0
1930: 26:	» Malmö	2	3	1
1930: 32:	» Schonen, Limhamn	1	1	0
1930: 36:	» » »	3	3	0
1930: 40:	» Falsterbo	5	7	0
1930: 53:	» Skanör	4	4	0
1930: 56:	» »	25	27	1
1930: 71:	» Simrishamn	3	4	0
1930: 75:	» »	1	2	0
1930: 83:	» »	2	2	0
1930: 109:	» Schonen, Åhus	5	6	0
1930: 128:	» Visby	2	2	0
1930: 167:	» »	6	8	0
1930: 220:	» Kalmar	6	10	1
1930: 222:	» »	2	2	1
1930: 250:	» Insel Öland, Färjestaden	4	6	0
1930: 257:	» Småland, Nybro	6	6	1
1930: 286:	» Gothenburg, unter dem Namen *T. lacistophyllum* Dt. (Borgvall)	4	4	1
1930: 287:	» Gothenburg, unter dem Namen *T. brachyglossum* Dt.? (Borgvall)	6	6	1
	Obliqua.			
1930: 292:	*T. obliquum* Fr., Schweden: Insel Öland, Mörbylånga[1]	2	1?	10

[1] Inwieweit das schlechte Resultat bei Kastrationen dieses Biotypus auf die Kastrationsmethoden, die kleinen Blüten oder innere Ursachen zurückzuführen ist,

		Anz. kastr. Individuen	Positive Kastr.	Negative Kastr.
1930: 44:	*T. platyglossum* RAUNK., Schweden, Falsterbo	2	2	0
1930: 49:	» » » » »	2	6	1
	Vulgaria.			
1929: 1:	Leningrad, unter dem Namen *T. interruptum* DT. erhalten	2	3	2
1929: 3:	» unter dem Namen *T. copidophyllym* DT. erhalten	4	12	1
1929: 5:	» unter dem Namen *T. maculigerum* LINDB. FIL. erhalten	3	6	4
1929: 7:	» unter dem Namen *T. duplidens* LINDB. FIL. erhalten	2	6	0
1929: 8:	Roston Don, unter dem Namen *T. palustre* erhalten	6	19	2
1929: 10:	Leningrad, unter dem Namen *T. involucratum* DT. erhalten	2	4	2
1929: 11:	» unter dem Namen *T. parvuliceps* LINDB. FIL. erhalten	5	6	1
1929: 15:	Gorky, unter dem Namen *T. officinale* erhalten	4	8	1
1929: 17:	Bukarest, unter dem Namen *T. officinale* erhalten	3	7	1
1929: 19:	Roston Don, unter dem Namen *T. officinale* erhalten	6	9	6
1929: 26:	Schweden, Schonen, Ålabodarna	1	3	1
1930: 5:	» Lund	5	6	0
1930: 24:	» Schonen, Nybro	2	4	2
1930: 31:	» zwischen Malmö und Limhamn	?	2	2
1930: 33:	» Schonen, Limhamn	5	3	3
1930: 63:	» » Dalby	1	1	0
1930: 181:	» Insel Gotland, Roma	1	1	0
1930: 215:	» Kalmar	2	2	4
1930: 221:	» »	6	7	0
1930: 223:	» »	2	2	0
1930: 241:	» Insel Öland, Vickleby Alvar	2	2	1
1930: 245:	» » » » »	4	3	1
1930: 251:	» » » Färjestaden	5	10	0
1930: 256:	» Småland, Nybro	4	1	4
1930: 288:	» Gothenburg, unter dem Namen *T. obliquilobum* DT. (BORGVALL)	3	0	6
1930: 289:	» Gothenburg, unter dem Namen *T. umblycentrum*? (BORGVALL)	6	4	2
1930: 294:	» *T. fasciatum* DT.	?	1	3

wage ich noch nicht mit Bestimmtheit zu sagen. Ein von Gothenburg erhaltener Biotypus dieser Art hat sich indessen als triploid erwiesen (s. S. 52).

	Anz. kastr. Individuen	Positive Kastr.	Negative Kastr.
1930: 295: Schweden *T. longisquameum* LINDB. FIL. ..	2	2	1
1930: 296+300: » *T. patens* DT.	11	5	11
»Arjeploug» Nr. 5: Schweden, Pite lappmark, Arjeploug	1	2	0
» » 8 + 10: Schweden, Pite lappmark, Arjeploug	2	2	1
» » 12: Schweden, Pite lappmark, Arjeploug	1	1	0
»Jäckvik» 1: Schweden, Pite lappmark, Jäckvik	1	1	0
» 2: » » » »	1	1	0
» 4: » » » »	1	3	0
Spectabilia.			
1929: 12: Sodnas (unter dem Namen *T. lapponicum* KIHLM.)	12	22	1
»Arjeploug» Nr. 4: Schweden, Pite lappmark, Arjeploug	1	3	0
» » 6 + 9: Schweden, Pite lappmark, Arjeploug	2	1	3
»Peljekaise» » 3: Schweden, Pite lappmark, Peljekaise	1	1	0
» » 10: Schweden, Pite lappmark, Peljekaise	1	1	0
» » 11: Schweden, Pite lappmark, Peljekaise	1	1	0
» » 12: Schweden, Pite lappmark, Peljekaise	1	1	0
» » 13: Schweden, Pite lappmark, Peljekaise	1	1	0
»Vuoggatjolme» Nr. 1: Schweden, Pite lappmark, Vuoggatjolme	1	1	0
»Tjidtjak Bäck» » 2: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	1	0	1
» » 5: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	1	1	0
» » 7 + 14: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	2	1	1
» » 10: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	1	1	0
» » 17: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	1	1	0
» » 23: Schweden, Pite lappmark, Tjidtjak, im Birkengebiete	1	1	0
Ceratophora.			
1929: 13: Leningrad, unter dem Namen *T. fasciatum* DT. erhalten	?	7	8

CHROMOSOMENZAHLEN.

Bisher sind mit voller Sicherheit nur die Chromosomenzahlen der obenerwähnten sexuellen *Taraxacum*-Biotypen bekannt, also die Entdeckung ROSENBERGS von 8 haploiden Chromosomen bei *T. confertum* DT. und OSAWAS Feststellung von 8 haploiden Chromosomen bei *T. platycarpum* DT. Ausserdem liegen Untersuchungen vor von JUEL 1905, SCHKORBATOW 1909 (zitiert nach ROSENBERG 1917), OSAWA 1913, STORK 1920, SEARS 1922 und HEITZ 1926 über wahrscheinlich parthenogenetische Biotypen, deren Zahlen nicht mit voller Genauigkeit haben festgestellt werden können. So fand JUEL bei *T.* »*officinale*» 2n = ungefähr 26 (eines seiner eigenen Bilder zeigt jedoch sehr schön die somatische Zahl 24), OSAWA bei *T. albidum* DT. 2n=36—40, STORK bei *T.* »*erythrospermum*» 2n = 26—30, SEARS bei *T.* »*lævigatum*» 2n = ungefähr 26 und HEITZ bei *T.* »*officinale*» 2n = ungefähr 24.

Untersuchungen über die Chromosomenzahlen in Wurzelspitzen von parthenogenetischen *Taraxacum*-Biotypen liegen noch nicht in grösserer Ausdehnung vor und die obengenannten Zahlen dürften mit Ausnahme für die zwei diploiden Biotypen unsicher sein; die Chromosomen sind bei den Teilungen der Makro- und Mikrosporenmutterzellen klein und zusammengepackt und wenigstens in jenen Fällen, wo die Zählung in Pollenmutterzellen vorgenommen worden ist, dürften die Zahlen zufolge Halbierung und mangelhafter Paarung der Chromosomen zu hoch sein.

Sämtliche unten angegebenen Zahlen (ausser 1929: 4) sind bei somatischen Teilungen in Wurzelspitzen, nach Keimung der Samen zwischen Filtrierpapier, bestimmt worden. Fixiermittel war NAWASCHIN (5 T. 1 % CrO_3-Lösung, 2 T. 40 % CH_2O und $^1/_2$ T. konz. $HOCOCH_3$), die Färbung wurde mit HEIDENHAINS Eisenhämatoxylin ausgeführt. Die Schnitte waren 7—8 μ dick.

ARTEN AUSSERHALB DER GROSSEN APOMIKTISCHEN FORMENKREISE.

1929: 4: Aus dem botanischen Garten in Palermo unter dem Namen *T. minimum* BIG. erhalten, wahrscheinlich mit *T. megalorrhizon* HAND. MAZZ. identisch. Sexuell ..... n = 8

1929: 14 und 1929: 20: *T. serotinum* DC. Botanischer Garten Leningrad und Bukarest ..... 2n = 16

1930: 415: *T. bessarabicum* HAND. MAZZ. Ungarn: Szolnok prope Jasfényszaru, von PÉNZES ANTAL 1929 eingesammelt ..... 2n = 16

T. platycarpum DT. Von OSAWA untersucht. Gehört zum *Ceratophora*-Komplex? Sexuell ..... n = 8

T. confertum Dt. Von Rosenberg untersucht. Gehört zum *Vulgaria*-Komplex? Sexuell ..... n = 8
T. mongolicum Hand. Mazz.[1] Botanischer Garten, Leningrad ..... 2n = 32
T. Schroeterianum Hand. Mazz. Botanischer Garten, Stockholm. Apomiktisch? ..... 2n = 32
T. porphyranthum Boiss. Botanischer Garten, Gothenburg ..... 2n = 24

DIE GROSSEN APOMIKTISCHEN FORMENZENTRA.

Vulgaria.

1929: 1: Botanischer Garten, Leningrad, unter dem Namen *T. interruptum* Dt. erhalten ..... 2n = 24
1929: 11: Botanischer Garten, Leningrad, unter dem Namen *T. parvuliceps* Lindb. fil. erhalten ..... 2n = 24
1929: 21: Botanischer Garten, Leningrad, unter dem Namen *T. mimulum* Dt. erhalten ..... 2n = 24
1930: 149: Schweden: Insel Gotland, Visby ..... 2n = 24
1930: 182: » » » Klintehamn ..... 2n = 24
1930: 221: » Kalmar ..... 2n = 24
1930: 223: » » ..... 2n = 24
1930: 245: » Insel Öland, Vickleby Alvar ..... 2n = 24
1930: 289: » Gothenburg, unter dem Namen *T. amblycentrum* Dt.? erhalten (T. Borgvall) ..... 2n = 24
1930: 294: » Uppsala, *T. fasciatum* Dt. ..... 2n = 24
1930: 295: » » *T. longisquameum* Lindb. fil. ..... 2n = 24
1930: 296: » » *T. patens* Dt. ..... 2n = 24
1930: 306: » » *T. stenoschistum* Dt. ..... 2n = 24
1930: 316: » Nässjö, *T. pectinatiforme* Lindb. fil. ..... 2n > 20
1930: 350: » Småland, Barkeryd, *T. maculigerum* Lindb. fil. 2n = 24
1930: 351: » Uppsala, *T. involucratum* Dt. ..... 2n = 24
1930: 352: » » *T. latissimum* Palmgr.[2] ..... 2n = 24
1930: 400: Botanischer Garten, Stockholm, *T. duplidens* Lindb. fil. .. 2n = 24
1930: 401: » » » *T. macrocentrum* Dt. .... 2n = 24
1930: 402: » » Utrecht ..... 2n = 24
1930: 403: » » Liège ..... 2n = 24
1930: 404: » » Bukarest ..... 2n = 24

[1] Inwieweit diese Art apomiktisch ist oder nicht habe ich noch nicht untersuchen können. Von Handel Mazzetti wird sie als *T. ceratophorum* so nahestehend bezeichnet, dass sie nur auf Grund ihrer Verbreitung und klimatisch bedingten Merkmale als eigene Art aufzufassen ist. Bekanntlich sind die Handel Mazzetti-schen Arten laut Dahlstedt Komplexe von oft sehr verschiedenen Biotypen, die als selbständige Arten zu betrachten sind. Trotz ihrer Chromosomenzahl, die von der von *Ceratophora* nicht spezifisch verschieden ist, reihe ich sie bis auf weiteres in diese Gruppe ein.

[2] Die Biotypen 1930: 294 bis 1930: 352 habe ich von dem hervorragenden Kenner der *Taraxacum*-Flora Schwedens Herrn G. Haglund, Uppsala, bekommen, und sie sind deshalb als richtig bestimmt zu betrachten.

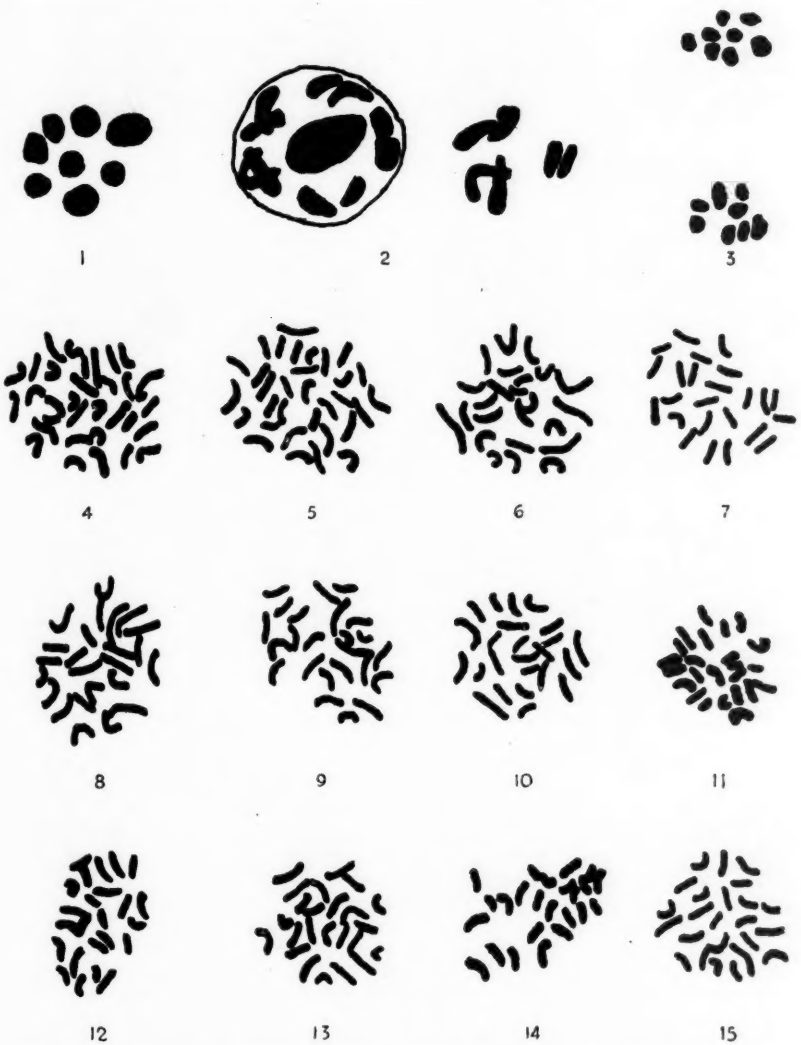

Fig. 1—15. — *1*: *T. minimum*, heterotypische Metaphase. 2: Diakinese in zwei Schnitten. *3*: heterotypische Anaphase. *4*: *T. Schroeterianum* HAND. MAZZ. *5*: *T. mongolicum* HAND. MAZZ. *6*: *T. porphyranthum* BOISS. *7*: *T. obliquum* FR. *8—19*: *Erythrosperma*. *8*: 1930, 408. *9*: *T. parnassicum* DT. *10*: 1930, 40. *11*: 1930, 71. *12*: 1930, 36. *13*: 1930, 81. *14*: 1930, 74. *15*: 1930, 90. — × 2100.

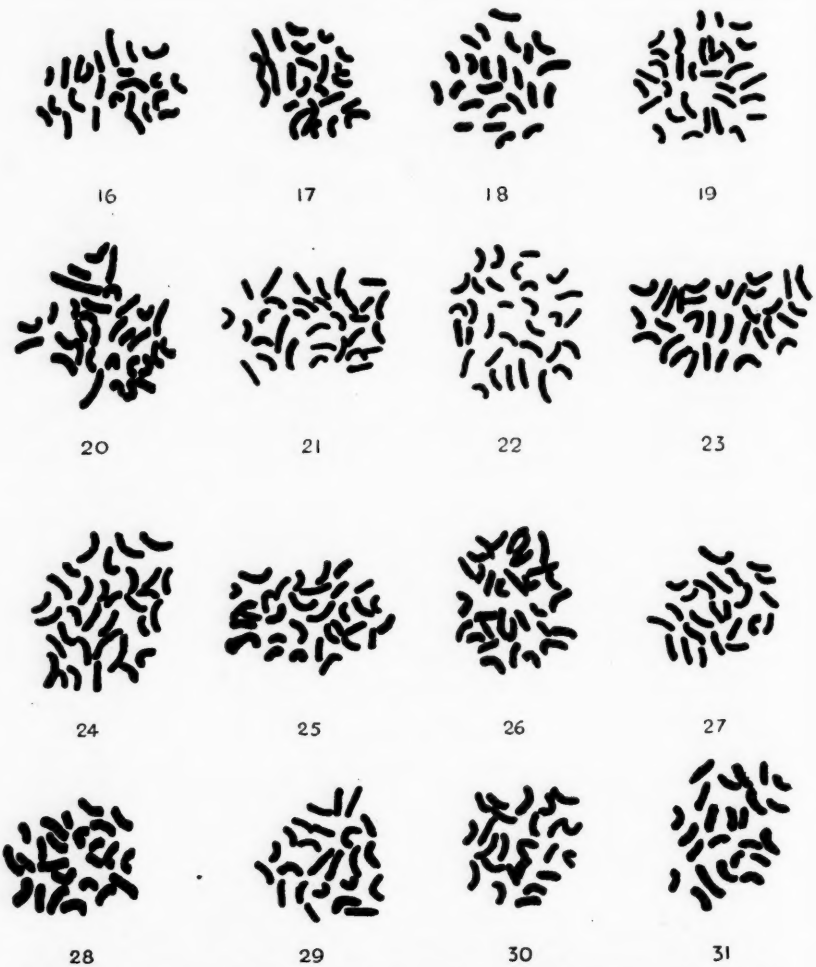

Fig. 16—31. — *16*: 1930, 96. *17*: 1930, 109. *18*: 1930, 250. *19*: 1930, 128. *20—25*: *Spectabilia*. *20*: 1930, 411. *21*: 1930, 304. *22*: 1930, 412. *23*: 1930, 305. *24*: 1930, 417. *25*: 1930, 409. *26—27*: *Ceratophora*. *26*: 1930, 413. *27*: 1930, 416. *28—31*: *Vulgaria*. *28*: 1929, 1. *29*: 1930, 406. *30*: 1929, 21. *31*: 1930, 149. — × 2100.

1930: 405: Botanischer Garten, Brünn ..... 2n = 24
1930: 406: » » Pavia ..... 2n = 24
1930: 407: » » Ventimiglia ..... 2n = 24
1930: 409: Schweden: Halland, Släp, unter dem Namen *T. croceiflorum* DT.? erhalten (T. BORGVALL) ..... 2n > 20

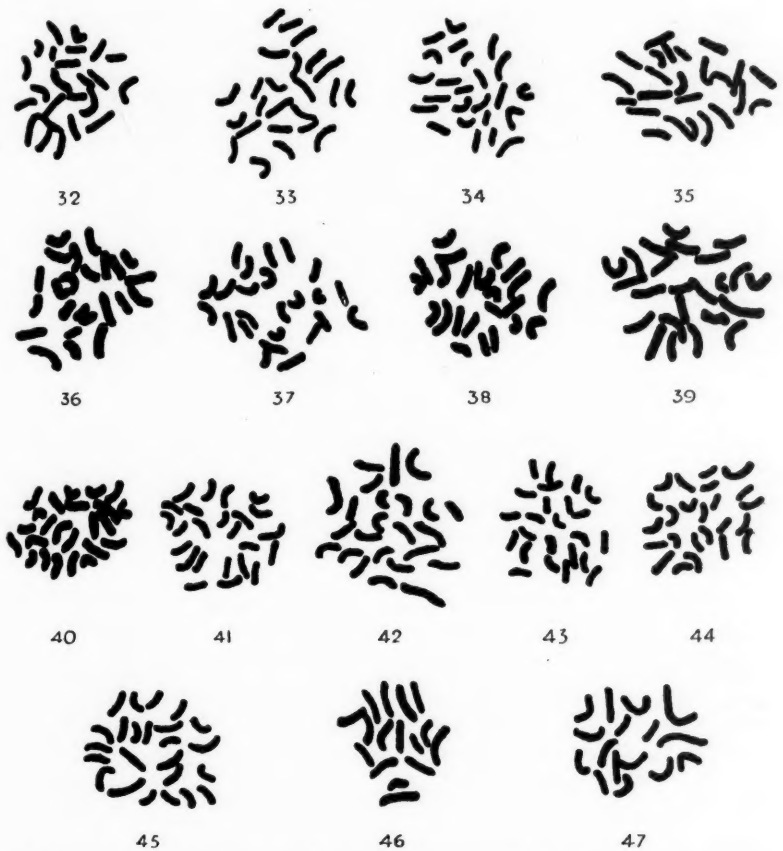

Fig. 32—47. — *32*: 1930, 289. *33*: *T. fasciatum* DT. *34*: *T. longisquameum* LINDB. FIL. *35*: *T. stenoschistum* DT. *36*: *T. maculigerum* LINDB. FIL. *37*: *T. involucratum* DT. *38*: *T. latissimum* PALMGR. *39*: *T. macrocentrum* DT. *40*: *T. duplidens* LINDB. FIL. *41*: 1930, 402. *42*: 1930, 403. *43*: 1930, 404. *44*: 1930, 405. *45*: 1930, 407. *46*: *T. serotinum* DC. *47*: *T. bessarabicum* HAND. MAZZ. — × 2100.

Erythrosperma.

1930: 1:	Schweden:	Malmö	2n = 23—24
1930: 36:	»	Schonen, Limhamn	2n = 24
1930: 40:	»	Falsterbo	2n = 24
1930: 48:	»	»	2n > 20
1930: 56:	»	Skanör	2n = 24
1930: 71:	»	Simrishamn	2n = 24
1930: 74:	»	»	2n = 24

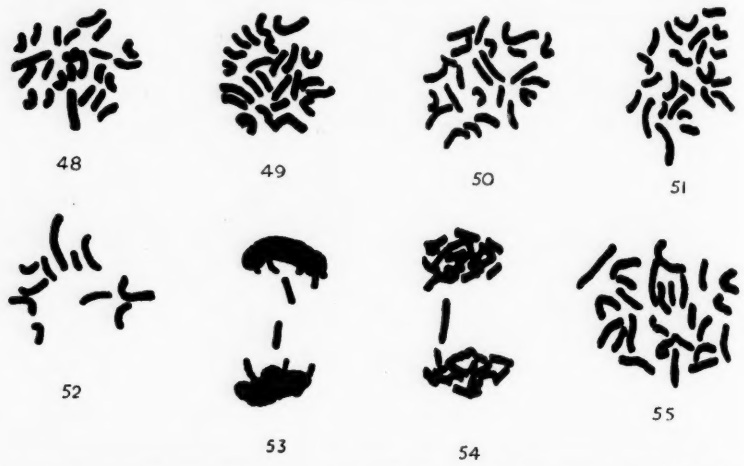

Fig. 48—55. — *48—51*: *Vulgaria*. *48*: 1929, 11. *49*: 1930, 182. *50*: 1930, 221. *51*: 1930, 223. *52*: *T. cornutum* Dt. *53*: 1930, 125. Homotypische Anaphase. *54*: *T. macrocentrum* Dt. *55*: *T. macrocentrum* Dt. Kernplatte mit 26 Chromosomen. — × 2100.

1930: 81: Schweden, Simrishamn ..... 2n = (23—)24
1930: 90: » Schonen, Åhus ..... 2n = 24
1930: 96: » » » ..... 2n = 24—25
1930: 109: » » » ..... 2n = 24
1930: 128: » Insel Gotland, Visby ..... 2n = 32
1930: 250: » » Öland, nahe Färjestaden ..... 2n = 24
1930: 410: *T. parnassicum* Dt. Botanischer Garten, Stockholm, aus Samen von Griechenland ..... 2n = 24
1930: 408: Schweden: Gothenburg, *T. lacistophyllum* Dt. (T. Borgvall) 2n = 24

Obliqua.

T. obliquum Fr. Schweden: Halland, Askim (T. Borgvall) ..... 2n = 24

Palustria.

T. lanceolatum Poir. Deutschland: Landau. Eingesammelt 1929 von Ch. d'Alleizette ..... 2n = 32

Spectabilia.

1930: 304: Schweden: Pite lappmark, Tjidtjak ..... 2n = 32
1930: 305: » » » » ..... 2n = 32
1930: 318: » » » Vuoggatjolme[1] ..... 2n = 40?

[1] Dieser interessante Biotypus ist wahrscheinlich pentaploid. In mehreren Kernplatten habe ich eine Zahl von ungefähr 40 gefunden; die schönste Platte zeigte jedoch nur 39 Chromosomen, da aber die ersten Schnitte dieses Biotypus leider nur 7 *u* dick waren, ist es möglich, dass ein Chromosom weggeschnitten worden ist.

1930: 409: Botanischer Garten, Edinburgh, unter dem Namen *T. officinale* erhalten. Ist jedoch unzweideutig eine *Spectabilia*-Form ..... 2n = 32

1930: 411: Botanischer Garten, Kowno, unter dem Namen *T. lapponicum* KIHLM. (= *T. croceum* DT.?) erhalten ..... 2n = 32

1930: 412: Botanischer Garten, Gothenburg, unter dem Namen *T. croceum* DT. erhalten ..... 2n = 32

1930: 417: Botanischer Garten, Leningrad, unter dem Namen *T. nævosiforme* DT. erhalten ..... 2n = 32

Ceratophora.

1930: 413: *T. brachyceras* DT., Botanischer Garten, Oslo, aus Samen von Grönland ..... 2n = 32

1930: 416: *T. cornutum* DT., Botanischer Garten, Riga[1] ..... 2n = 24

T. albidum DT. Von OSAWA untersucht. Siehe DAHLSTEDT 1907 a, S. 3 u. 14 ..... 2n = (36—)40?

Arctica.

1930: 414: *T. arcticum* TRAUTW., Botanischer Garten, Oslo, aus Samen von Grönland. Ob diese Art apomiktisch ist oder nicht, wage ich noch nicht zu sagen; auf Grund der schlechten Pollenbildung ist sie wohl so zu deuten. Die Zahl liegt zwischen 44 und 49, ist also hexaploid (oder jedenfalls hyperpentaploid).

Aus diesen Zahlen geht es also hervor, dass *Taraxacum* sich zytologisch dadurch wie die früher untersuchten Gattungen *Rosa* (TÄCKHOLM 1922), *Potentilla* (MÜNTZING 1931) und *Archieracium* (ROSENBERG 1927) verhält, dass sie polyploide Reihen mit gerade Multiplen bildet. Das Vorkommen von hochchromosomigen Biotypen ist jedoch selten, aber ihre Anzahl dürfte wahrscheinlich bei sorgfältigerer Untersuchung von arktischen und hochalpinen Formen vermehrt werden, und auch innerhalb *Archieracium*, wo ROSENBERG Zählungen der Chromosomenzahlen von 21 Repräsentanten ausgeführt hat, werden wahrscheinlich hochpolyploide entdeckt werden, besonders vielleicht in der vielförmigen und schönen *alpinum*-Gruppe. Ein Umstand, das Interesse besitzt, ist dass die Hauptmenge apomiktischer *Taraxaca* und *Archieracia* (auch *Erigeron*, *Eupatorium*, *Artemisia*) triploid und in geringerer Ausdehnung tetraploid sind, während unter den *Rosaceen* noch keine triploiden Apomikten angetroffen worden sind; innerhalb des *Rosa canina*-Kom-

Bei einem pentaploiden Biotypus ist natürlich eine Schnittdicke von 7 μ im allgemeinen zu klein.

[1] Ob diese Art richtig bestimmt ist und wirklich aus Norwegen stammt, habe ich noch nicht entscheiden können. Auf Grund der Form der Cotyledonen, des Aussehens der Rosettenblätter und der Fruchtgrösse ist sie jedoch gar nicht dem *Vulgaria*-Komplex zuzurechnen.

plexes kommen pentaploide und weniger allgemein tetra- und hexaploide Zahlen vor, europäische apomiktische *Eubati* weisen noch keine bekannten spontanen Triploiden auf (CRANE und DARLINGTON 1927; eigene vorläufige Mitteilung), und einerlei ist das Verhältnis bei *Potentilla* mit bis duodecaploiden Biotypen. Vielleicht kann dies auf die verschiedene Intensität der Kreuzungsprozesse oder ungleiche genotypisch bestimmte Tendenz zur Erhöhung der Chromosomenzahlen innerhalb der fraglichen Gattungen zurückgeführt werden.

Interessant ist der Fund der zwei diploiden Arten *T. serotinum* und *bessarabicum* ausser den sexuellen diploiden *T. minimum*, *platycarpum* und *confertum*. Da sie beide gute und sehr charakteristische Formen mit grosser Verbreitung in Südosteuropa sind, liegt der Gedanke nahe, dass auch sie sexuell sein sollen, was natürlich vor Eintritt der Blütezeit nicht entschieden werden kann[1]. Gleichartige Verhältnisse bei *Taraxacum* bestehen bei *Hieracium*. Auch dort besitzen die sexuellen Arten *H. umbellatum* und *auricula* die diploide Chromosomenzahl (OSTENFELD, ROSENBERG), während die parthenogenetischen und aposporen *Archieracium*- und *Pilosella*-Formen triploid, tetraploid oder hypertetraploid sind. Auch bei *Antennaria* ist die sexuelle Art *dioica* diploid, *alpina* dagegen tetraploid (JUEL, HOLMGREN) und bei *Eupatorium*, *Erigeron* und *Artemisia* sind die apomiktischen Formen triploid (HOLMGREN, CHIARUGI). Die einzige Ausnahme unter den *Compositeen* bildet die nur wenig untersuchte Art *Chondrilla juncea* (ROSENBERG 1912) mit der diploiden (?) Chromosomenzahl, trotzdem sie sich bei der Makrosporenteilung wie *Taraxacum* verhält. *Wahrscheinlich ist, dass es im südöstlichen Europa und Asien eine Reihe von sexuellen diploiden Arten gibt*, und vermutlich werden auch sexuelle Tetraploide entdeckt werden, die zum Entstehen sowohl der schwarz- und graufrüchtigen *Vulgariæ* als auch der rotfrüchtigen *Erythrospermæ* (des *lævigatum*-Komplexes) beigetragen haben. *Dass es ausserhalb der grossen apomiktischen Formenzentra auch parthenogenetische Biotypen gibt, zeigen* RAUNKIÆRS *Kastrationsresultate bei T. obovatum und glaucanthum* (= *dissectum nach* HANDEL MAZZETTI) *und auch mein Fund des triploiden T. porphyranthum* BOISS., sämtliche wohlcharak-

[1] Nachdem Vorstehendes geschrieben war, habe ich Gelegenheit gehabt, Kastrationen in grossem Massstabe (ungefähr 30 Körbe) von der obenerwähnten diploiden Art *T. serotinum* auszuführen, und es hat sich herausgestellt, dass sie wie erwartet sexuell war; auch waren bei der heterotypischen Metaphase 8 Doppelchromosomen zu sehen. *T. bessarabicum* hat freilich noch nicht geblüht, aber durch diesen letzten Fund scheint die Vermutung, dass auch es sexuell ist, noch mehr bekräftigt.

terisierte Biotypen; der letztgenannte weicht durch die glänzend grünen, lederartigen Blätter mit ihrer eigentümlichen Form, das Aussehen der Achänien und die Blütenfarbe höchst bedeutend von anderen Formen in meinen Kulturen ab.

CHROMOSOMENZAHLEN UND SEKTIONEN.

Um das ursprüngliche *T. croceum* DT. (= *lapponicum* KIHLM.?) sind mit der sorgfältigen Erforschung der *Taraxacum*-Flora Skandinaviens Formen gruppiert worden, die mit demselben — trotz der Vielförmigkeit — eine morphologisch und biologisch einheitliche Gruppe bilden, und von Repräsentanten des verwandten *Vulgaria*-Komplexes morphologisch durch sowohl quantitative als qualitative Eigenschaften[1] getrennt sind. Von Interesse ist hier den Unterschied zwischen den Chromosomenzahlen zu konstatieren: während alle *Vulgariæ* triploid sind, ist die Hauptmenge *Spectabiliæ* tetraploid, ein vereinzelter deutlich pentaploid. *Spectabilia* besitzt ein einhetliches Verbreitungsgebiet, das den nördlichen Teil Fennoskandias, hauptsächlich das alpine und subalpine Gebiet, umfasst und hat Repräsentanten in Schottland, auf den Färöinseln, Island, Grönland und an den Ufern des Weissen Meers entlang (DAHLSTEDT 1912). Weiter nach Osten kommen sie nicht vor, wie auch nicht in den Alpen und übrigen europäischen Gebirgsgegenden. Wegen der relativ einheitlichen Eigenschaften und Verbreitung der Gruppe scheint es mir, als wäre DAHLSTEDTs Auffassung derselben als eine besonders für Fennoskandia charakteristische Gruppe von wahrscheinlich präglazialer Herkunft berechtigt.

Zu dieser Gruppe rechnet DAHLSTEDT auch eine Anzahl Formen mit bedeutend südlicherem Verbreitungsbereich und in meinen Kulturen hervortretenden abweichenden Eigenschaften, welche die Einheitlichkeit stören, nämlich *T. maculigerum* LINDB. FIL., *præstans* LINDB. FIL. *Nordstedtii* DT., *Larsonii* DT. und *polium* DT., unter denen das Vorkommen des *T. Nordstedtii* von der ganzen Gruppe dadurch abweicht, dass es auch Böhmen, das nördliche Deutschland, England und einige Gegenden Frankreichs umfasst. *T. maculigerum* und *præstans* stehen gemäss DAHLSTEDT nordschwedischen *Spectabiliæ* so nahe, dass sie »aus einem von diesen in verhältnismässig später Zeit ausgebildet worden sind». (Von mir ins Deutsche übersetzt.) Diese

[1] Über diese Verhältnisse werde ich in einer späteren Veröffentlichung berichten, wo ich auch den Wert des Agamospeziesbegriffes TURESSONS für diese Formenkreise klarlegen werde.

Annahme kann ich unwahrscheinlich machen; *denn da das apomiktische T. maculigerum 24 Chromosomen besitzt, scheint es mir unmöglich, dass es aus den 32-chromosomigen Spectabiliæ* weder durch vegetative Mutation noch durch sexuelle Spaltung mit Senkung der Chromosomenzahl verbunden hervorgegangen sein kann. Auch scheint es mir nach DAHLSTEDTs Auseinandersetzung nicht zu *Vulgaria* geführt werden zu können, wo es auch von DAHLSTEDT früher eingereiht worden ist (z. B. DAHLSTEDT 1911), *sondern es soll mit vollem Recht in eine neue Gruppe, T. maculigerum-Gruppe, eingeordnet werden.* DAHLSTEDT selbst proponiert 1911 dieses Verfahren. *Dieser Gruppe soll also dasselbe Alter als den Spectabilia- und Vulgaria-Komplex zugeschrieben werden,* und von dem Standpunkte der dafür eintritt, dass die Parthenogenesis in triploiden und hochpolyploiden Gattungen als eine Folge- oder Begleiterscheinung von Kreuzungen zwischen oft verschiedenchromosomigen Arten oder Biotypen zu betrachten ist (ERNST, ROSENBERG, TÄCKHOLM), und dass somit die triploiden *Vulgariæ* durch Hybridisierung zwischen Diploiden und Tetraploiden und die tetraploiden *Spectabiliæ* zwischen Tetraploiden gegenseitig entstanden sind, ist es natürlich sich zu denken, *dass diese Formen, deren Eigenschaften eine Verschmelzung zwischen Vulgaria- und Spectabilia-Kennzeichen bilden, und deren führende Form triploid ist, aus Kreuzungen zwischen Repräsentanten der tetraploiden Spectabiliæ einerseits und einigen der diploiden Ursprungsformen der Vulgariæ andererseits hervorgegangen sind.* Wahrscheinlich geschah dies an den Aussenrändern für die Verbreitung der sexuellen Ur-*Spectabiliæ,* wo diese und sexuelle Diploide zusammengetroffen sind.

Eine Formengruppe die in Skandinavien auf Grund ihrer charakteristischen Eigenschaften und wohlabgegrenzten Stellung einen Sonderplatz einnimmt, ist *Palustria*; durch die kurzen, breiten und hautversehenen Deckblätter, die grossen Früchte und die abweichende Blattform bildet sie einen Komplex von Formen, die wenigstens in Nordeuropa ohne Übergänge zu *Vulgaria* vollkommen isoliert stehen (siehe Fussnote S. 55). In der Literatur gibt es jedoch auch Angaben über Formen die morphologisch teils in der Mitte, teils mehr oder weniger nahe der einen oder anderen Gruppe stehen und die Auffassung von *T. paludosum* (= *palustre* im weiteren Sinne) hat im Laufe der Zeiten sehr gewechselt.

Viele sehen in ihm nur eine Abart von *T. vulgare*, in das es laut ihrer Meinung unter »günstigen Verhältnissen» übergehen kann (KOCH, ASCHERSSON-GRÆBNER, auch HANDEL MAZZETTI), andere sehen in ihm

eine besondere, wohlcharakterisierte Art, die mit dem *Vulgaria*-Komplex durch (hybridogen entstandene?) Zwischenformen verbunden ist (z. B. FOCKE vielerorts, VOLLMANN); dass es jedoch auch in alten Zeiten Verfasser gab, welche die isolierte Stellung des *Palustria*-Komplexes betonten, zeigt z. B. MARSSON (1869) der sagt: »Dass die Pflanze spezifisch verschieden von *T. officinale* ist, beweisen die grosse Bestände in denen sie hier in Millionen von Exemplaren im ersten Frühling die Strandwiesen bedeckt, ohne Uebergänge zu *T. officinale* zu zeigen». *Ein Übergang des einen in das andere durch Änderung der äusseren Bedingungen oder durch Mutieren scheint mir mit den verschiedenen Chromosomenzahlen der zwei Gruppen unmöglich*; eher ist wohl die Auffassung richtig, die im *Vulgaria*-Komplex einen Schwarm von formæ apomiktæ sieht, denen meistens gemeinsamer Ursprung zuzuschreiben ist. Einige von ihnen, wenn sie wirklich Mittelformen zwischen den zwei Komplexen wären, könnte man dagegen auf Kreuzungen zwischen den Ureltern der *Vulgaria*- und *Palustria*-Gruppen zurückführen, und Selektionsverhältnisse sollten dann dazu beigetragen haben, im nördlichen Verbreitungsgebiete der *Palustria*-Gruppe die zwei Komplexe zu isolieren und die Bildung von Agamospezies ohne Zwischenformen zu bedingen, wie es ja schon bekannt ist, dass pollenführende *palustre*- und *balticum*-ähnliche Biotypen gegen Norden immer mehr eliminiert werden und in Skandinavien pollenmangelnde *palustre* und *balticum* alleinherrschend sind (DAHLSTEDT 1907 b).

DIE FORMENBILDUNG.

Während der letzten Jahre haben zytologische Studien über die apomiktischen Formenkreise dazu beigetragen, die wahrscheinlich grosse Bedeutung der Hybridisierungen für das Eintreten von Apomixis und das Entstehen der polyploiden Reihen klarzulegen. Es hat sich immer mehr die Auffassung geltend gemacht, dass die Apomixis auf eine Serie von zusammenwirkenden Umständen, Kombination von Erbanlagen, Hybridisierung, Polyploidie (WETTSTEIN 1927, SCHNARF 1929) beruht. SCHNARF meint, dass innerhalb apomiktischer Gattungen schon bei den sexuellen Arten Anlagen für Apomixis vorhanden sind, obgleich diese hier nur sehr wenig zur Geltung kommen. In Kreuzungen, wo Anlagen für Apomixis vereint werden und zufolge Chromosomenstörungen ♂- oder ♀-Sterilität eintritt, wird die Möglichkeit für die apomiktisch eingerichteten Makrosporen oder die diploiden Nuzelluszellen ohne Konkurrenz Entwicklung zu erreichen, natürlich bedeutend

grösser als bei sexuellen Arten mit reichlichem Pollenvorkommen und ohne Störungen entstandenen Eizellen.

Über die Art und Weise, auf der die Formenbildung stattgefunden hat, herrschen noch verschiedene Meinungen. Folgendes zunächst mit Rücksicht auf die triploiden *Taraxaca* und *Archieracia* aufgestellte Schema veranschaulicht die verschiedenen Möglichkeiten für die Formenbildungswege und Entstehung der Apomixis als dominante oder rezessive Eigenschaft (für andere Chromosomenzahlen ergibt sich natürlich eine analoge Betrachtungsweise):

I. Die Triploidie ist durch Autopolyploidie entstanden. Die Apomixis ist eine dominante Erscheinung. Formenbildung wie II.

II. Die Triploidie ist durch Kreuzungen diploid × tetraploid entstanden. Die Apomixis ist dominant, ev. von mehreren Faktoren bedingt. Die Formenbildung beruht auf: 1) Chromosomenaberrationen (somatisches Nichttrennen); 2) Deficiency-Mutationen; 3) Genmutationen. Die Triploiden sind als vegetative F_1-Abkömmlinge zu betrachten; 4) Sekundäre Kreuzungen und Spaltungen. Die Formenbildung hat hier F_2-Charakter.

III. Die Triploidie ist durch Kreuzungen diploid × diploid, Bildung von Restitutionskernen und gegenseitige Wiederkreuzung oder mit sexuellen Diploiden entstanden. Die Apomixis ist eine rezessive (?) Erscheinung. Die Formenbildung hat F_2-Charakter.

Dass die Autopolyploidie in gewissen Fällen auch bei diesen Pflanzengattungen vorkommen kann, ist wohl nicht zu bezweifeln, aber ihre Bedeutung dürfte in apomiktischen Gruppen von stark heterogener Zusammensetzung recht begrenzt sein. Für die Entstehung gewisser hochpolyploider *Festuca ovina*- (TURESSON 1930) und einiger *Potentilla*-Typen (MÜNTZING 1931) machen die genannten Verfasser die Autopolyploidie verantwortlich, und bei einer der untersuchten *Potentillæ* wird diese Ansicht dadurch gestützt, dass bei der Reduktionsteilung Quadri- und Hexavalente gebildet werden, was deutlich von mehr oder weniger homologen Chromosomengruppen abhängig ist.

Schon HEITZ (1926) hatte gefunden, dass die Chromosomen desselben *Taraxacum*-Biotypus verschieden gross sind, einen Fund, den ich bestätigen kann. In seinem Bild 1 *f* sieht man acht grössere Chromosomen und unter diesen eines, das entschieden länger als die anderen ist. Wegen der allmählichen Übergänge in der Grösse der Chromosomen ist ein deutlicher Unterschied nur ausnahmsweise vorhanden, und zahlreichere direkte Messungen der Chromosomenlänge habe ich noch nicht ausgeführt. In einigen vereinzelten Fällen sind doch qualitative

Unterschiede wahrgenommen worden, am leichtesten natürlich in den diploiden Arten. Wie aus Fig. 1 hervorgeht, gibt es bei *T. minimum* unzweideutig ein grosses Chromosomenpaar (das übrigens wegen seiner Grösse den Eindruck eines Quadrivalentes macht), bei *T. bessarabicum* (Fig. 47) sind zwei Chromosomen grösser und bei *T. serotinum* (Fig. 46) zwei kleiner als die anderen. Auch in *T. platycarpum* ist nach OSAWAS Bilder zu urteilen ein grosses Chromosomenpaar vorhanden (siehe OSAWA, Tafel 37, Fig. 17).

Diese Beobachtungen sind von Interesse, denn wenn die triploiden (oder tetraploiden) Biotypen durch Autopolyploidie aus diploiden sexuellen und innerhalb gewisser Grenzen homozygoten Arten entstanden und dann durch Genmutationen in die zahlreichen Kleinspezies aufgeteilt worden wären, sollte natürlich bei den Triploiden (resp. Tetraploiden) jede Grössenklasse dreimal (resp. viermal) repräsentiert werden. *Bis jetzt untersuchte, deutliche Fälle gibt es nur wenige, aber sämtliche berechtigen zu der Annahme, dass Allopolyploidie die Ursache der Chromosomenvermehrung ist. So z. B. besitzt 1929: 11* (Fig. 48) *unzweideutig zwei ansehnliche Chromosomen und bei 1930: 416* (Fig. 27 u. 52) *wurde in mehreren Kernplatten ein Chromosom wahrgenommen, das bedeutend länger als die übrigen war. Gleichartig war das Verhältnis bei 1930: 221 und 223* (Fig. 50 u. 51), und — mit Reservation — bei 1930: 182 und *T. porphyranthum*. Diese interessanten Tatsachen hoffe ich später näher untersuchen zu können.

Aberrationen bei den somatischen Teilungen in den Embryonen oder bei der Restitutionskernbildung der Makrosporenmutterzellen kommen wohl sicher vor, scheinen aber wegen der geraden Zahlen keine grosse Rolle für die Formenbildung gespielt zu haben. Selbst habe ich bei Teilungen in Wurzelspitzen ein paar Fälle von Chromosomenunregelmässigkeiten wahrgenommen. Fig. 53 veranschaulicht eine Teilung des *Vulgaria*-Biotypus 1930: 125 (von Gotland), Fig. 54 eine solche des *T. macrocentrum* mit verspäteten Chromosomen, und Fig. 55 zeigt eine Platte von *T. macrocentrum* mit unzweideutig 26 Chromosomen, und auch bei 1930: 403 glaube ich gleichartiges gesehen zu haben. Auch FROST und MANN (1924) und DARLINGTON (1926) beschreiben analoge Störungen unter normalen Bedingungen, und vereinzelte Male dürften wohl auch neue Biotypen auf diesem Wege entstehen können.

Über die Bedingungen und Häufigkeit vegetativer Gen- und Deficiency-Mutationen innerhalb des Pflanzenreiches wissen wir nur wenig; auch in einem genetisch wohluntersuchten Material treten sie dann

und wann auf. MURBECK (1904), SAMUELSSON (1910) und TÄCKHOLM (1922) nehmen für die Formenbildung in den apomiktischen Gattungen (mit Ausnahme von *Rubus* und *Hieracium Pilosella,* wo Kreuzungen experimentell ausgeführt sind), Genmutationen an, und OSTENFELD hat zwei zur schwer klarzulegenden Formengruppe *Hieracium tridentatum* gehörigen Formen erhalten und glaubt, dass sie in dieser Weise gebildet worden sind. TÄCKHOLM nahm sogar an, dass die grosse Heterozygotie die Mutationsfrequenz befördern sollte. *Innerhalb Taraxacum scheint die Formenbildung durch Gen- und Blockmutationen mit primären Kreuzungen als Ursache der Polyploidie verbunden als die wahrscheinlichste.* Bedenkt man, dass ein einziges Individuum jährlich cirka 4,000 Achänien gibt, und ein gewisser Biotypus vielleicht in einer Individuenzahl von 10,000 vorkommt, so werden jedes Jahr 40 Millionen und während 100 Jahren 4 Milliarden Früchte gebildet, und da die Heterozygotie in der Hinsicht die Formenbildung befördert, dass die Verlustmutanten leichter sichtbar werden und grösseren Selektionswert als in ganz homozygoten reinen Linien haben, glaube ich, diesen Formenbildungsweg als recht plausibel bezeichnen zu können. Für eine endgültige Lösung dieses Problems sind indessen — wie immer — experimentelle Forschungen unvermeidlich, und solche sind jetzt auch begonnen worden.

SUMMARY.

1. Castration experiments have been made in a number of forms belonging to the groups *Vulgaria, Erythrosperma, Obliqua, Spectabilia, Ceratophora.* The always positive results show that sexual biotypes must occur very infrequently if they exist at all.

2. The group *Vulgaria* is triploid ($2n = 24$), *Erythrosperma* is triploid and occasionally tetraploid, *Palustria* is tetraploid, *Obliqua* is triploid, *Spectabilia* is tetraploid and occasionally pentaploid, *Ceratophora* is triploid and tetraploid, and *Arctica* is probably hexaploid.

3. Three diploid species outside the great apomictical groups, *T. minimum* from Palermo (*megalorrhizon* HAND. MAZZ.?), *T. serotinum* DC. and *T. bessarabicum* HAND. MAZZ. have been found. The two first are sexual, the latter probably is.

4. A new group, *T. maculigerum* group, is established, enclosing a number of forms which are intermediate between the groups *Spectabilia* and *Vulgaria* and whose main form is triploid.

5. The opinion often expressed by taxonomists that *T. paludosum* SCOP. is only a variation of *Vulgaria* formed by external ecological

factors or »mutations» must be wrong. On the contrary, the two groups are to be regarded as well separated agamospecies, each in its northern territory containing a group of formæ apomictæ and without transitions between them.

6. Differences in size between the chromosomes are shown in the diploid and apomictical forms. Four certain cases confirm the opinion of allopolyploidy as the cause of polyploidy.

7. In *Taraxacum* the formation of new forms by means of gene- and blockmutations associated with primary crossings as the cause of polyploidy seems to be the most plausible explanation.

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A THEORY ON THE CYTOLOGICALLY IRREGULAR SPECIES VIOLA CANINA L.

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INTRODUCTION.

AMONG the very interesting cases recently reported of cytologically irregular species showing structural hybridity is also according to CLAUSEN (1931 a) to be included *Viola canina* L. The author arrives at the following conclusions in his cytological investigation of this species from several Danish localities: *Viola canina* is cytologically irregular with oscillating number of chromosomes. Besides the 20 bivalents a varying number of extra chromosomes and fragments are found. The most regular type, »the Tisvilde population», has $2n = 40$ chromosomes plus 3 diminutive chromosomes or fragments, but other types, specially one belonging to var. *lucorum*, are extremely irregular. Most probably, *canina* maintains itself as a cytologically irregular species through constant intercrossing between different types belonging to the species.

These conclusions are based on a cytological investigation of meiosis of three populations from Northern Sjælland and on a pollen inspection of two more types from another locality of Sjælland and from Småland in Sweden. CLAUSEN is evidently inclined to extend these conclusions to the species as such in all its wide distribution. Considering its many variations and the fact that several ecologically distinct types exist, of which at least those on rocky ground, sea-shores and moors undoubtedly are natural inhabitants, long ago established in these localities, one may object that this conclusion is perhaps a little too wide. CLAUSEN accordingly invites cooperation with cytologists, who have access to material of the species from other localities, and this is, no doubt, the right way to a thorough understanding of a case like this.

The material of the present little study was collected mainly with the object of comparing the diminutive chromosomes reported to be present in *Viola canina* with those sometimes found in *Ranunculus acris* and certain *Primula* species, which are under investigation (BRUUN 1931). This object failed so far as the type fixed for this purpose has got neither fragments nor extra chromosomes. As there are reasons

to suppose that the plants fixed are different individuals and not a single clone, it is rather surprising that, unlike the state of things in Denmark, all the plants studied have apparently identical chromosomal constitution and, as will be shown below, an euploid number of chromosomes.

METHODS AND MATERIAL.

For investigation of these irregular species, where the point in question is getting a general survey of the chromosomal condition of the largest possible numbers of individuals of a certain species or race in a district, the following methods have been worked out. NAWASCHIN (1926) has used a similar, though more tedious method, in his extensive *Crepis* investigation. Seeds are collected from a great number of plants, a little from each. They are germinated between moist blotting paper, and from each seedling only one root tip is fixed, the tap-root. In inbedding in paraffin-wax, the tips are arranged parallel to each other in small bundles of 6 to 10. Two or three such bundles are easily mounted on the same slide. It is therefore possible to investigate some 12 to 30 plants on a single slide. With a minimum of work in preparing the slides, one gets a maximum of material, which, as each plant is only represented with a single root, may be the foundation of statistical calculation. The process of cell division is usually active enough to yield a sufficient number of cell plates for the determination of the chromosome number. This method has been successfully practised on the particularly variable *Ranunculus acris,* which will be discussed on another occasion.

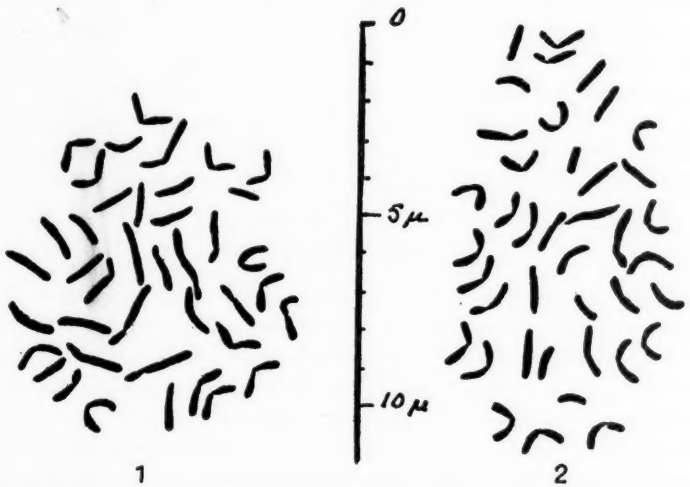
Unfortunately this statistically superior method could not be used in the present investigation as no ripe seeds were at hand when the material was collected last spring. Instead some 40 plants were brought home from a dry, open pine heath at Rickomberga near Uppsala, Sweden. A part of the plants were sent to Dr. J. CLAUSEN, then in Copenhagen, another part were dried, and the rest were potted close together. This Rickomberga population is not quite homogeneous, however, as some of the largest plants are *canina* × *Riviniana.* Mr. ERNST NORDSTRÖM, who has kindly revised my dried specimens, has found them all, a doubtlessly hybrid plant excepted, to be *pure canina.* Unfortunately this heterogeneity was not noticed until quite recently, and therefore CLAUSEN has probably got some hybrids in his material as he identifies this form as *V. canina* var. *lucorum* REICHB. New roots were soon formed in the pot, and a great number of these were

fixed from different parts of the root lump. Thus it is possible that some occasional hybrid has been represented in the material. In the present study, however, no traces of hybridity have been found.

The fixative was a modified NAWASCHIN, consisting of equal parts of the standard solutions »A» and »B». »A» being 2 gr CrO_3, 20 cm^3 glacial acetic acid and 130 cm^3 H_2O and »B» 37 cm^3 commercial formalin deluted to 150 cm^3. Sections were cut 12 microns thick and stained in NEWTON's gentian violet-iodine.

CYTOLOGY.

The publication of the chromosome number n = 36 for *Viola canina* (CLAUSEN 1926, 1927), a figure which MIYAJI (1929) questioned on



Figs. 1—2. Somatic metaphases from root-tips of the Rickomberga type of *Viola canina*.

theoretical grounds, has later been corrected by the same author (CLAUSEN 1931) to n = 20, though actually this number has not been found, as there are always some extra chromosomes or fragments present. Thus *V. canina* is brought in line with the main part of the caulescent *Nominium*-Violets, which have 10 as a basic number. As already indicated, I am able to confirm the figure n = 20, as exactly 40 chromosomes have been found in all 38 roots investigated. Furthermore no difference whatever has been noticed between the chromo-

somal equipment of these roots, nor have any fragments or extra chromosomes been found. Thus this population from Rickomberga must be cytologically better balanced than any hitherto investigated, and therefore a short description of the chromosomes is given for eventual comparison with other populations.

The chromosomes are of unequal size (figs. 1 and 2), the longest being about double the length of the shortest. Furthermore there is a distinct difference in the place of the constrictions. About 20 chromosomes have median and several submedian constriction whilst in some chromosomes no constriction can be discerned. It is not possible for the present to give the idiogram in detail, since the chromosomes are so numerous that some of them are always bound to lie unfavourably, specially the central ones which generally do not show any bending at the point of constriction. The medially constricted ones are all of about the same medium size. Four chromosomes are distinctly longer than the rest (though this fact does not appear quite clearly from the figures on account of foreshortening) and have submedian constriction, which sometimes is extended, thus easily causing miscalculation of the chromosome number. The four smallest of the whole set are always among the chromosomes in which no constriction can be discerned.

DISCUSSION.

We are here dealing with a race of *Viola canina*, which forms a normal constituent of a more or less natural plant association, the pine heath. As similar populations are of common occurrence in such localities in the district, there is, although the species is highly influenced by cultivation, no reason to doubt that it has resided for some time in these localities and that it very likely has had rather plenty of time to stabilize. This is confirmed by the present investigation. Unfortunately meiosis has not been studied, as the season was too far advanced when the material was collected, and this means a severe limitation of my argument but, on the other hand, the violets are characterized by their power to transmit aneuploid numbers of chromosomes to their offspring without serious affect on viability and fertility. Thus the strongest cause of a rapid attainment of equilibrium is at least partly neutralized and accordingly violets have less chance than most other plants of attaining balance. The non-appearance of extra chromosomes and fragments in the whole of my material thus demonstrates a great deal about the cytological balance of the race in question. This

balance apparently is more undisturbed than in CLAUSEN's most regular type, the »Tisvilde type». The hypothetical hybrid origin of the Rickomberga race must be sought far back in the past.

The var. lucorum REICHB. — Prevailing opinion on the origin and taxonomic value of the var. *lucorum* is contrary to this view. CLAUSEN expresses his opinion in these terms (1931 b, p. 332): »Var. *lucorum* REICHB. grows on shady places, it is larger and also with larger and more cordate leaves; probably often of recent hybrid origin, sometimes partially sterile», and (p. 328) he explains that the *lucorum* types must not always be of the first generation hybrids, from which follows that what is usually brought together as var. *lucorum* is not a taxonomic unit, which has spread over its present range of distribution, but that forms appertaining hereto have arisen independently of each other. The var. *lucorum* is no doubt of polyphyletic origin; thus conclusions from one population must not be extended to others. As to the Rickomberga population, both its appearance in nature and its chromosomal conditions, in as far as studied, coincide in marking it as a taxonomic unit of high stability. *No doubt, it is pure canina.*

The species Viola canina L. — CLAUSEN takes into consideration that the many variations of *V. canina* might be of polyphyletic origin which have started from somewhat different crossings. But this possibility is considered less probable than that the species *canina* taken as a whole is monophyletic but (1931 a, p. 83) »maintains itself as a cytologically irregular species with an oscillating number of chromosomes through constant intercrossing between cytologically different types belonging to the species, and that it renews the irregularity through occasional outcrossing with *Viola Riviniana* and perhaps other related species». In my opinion this is very likely the case in most Danish populations (the reputed rôle of *Riviniana* crossings being left out of consideration as only pure *canina* is regarded here) but this is far from certainly true of *canina* from other parts of its wide distribution area, where long established and well balanced populations, no doubt, exist.

According to Mr. NORDSTRÖM *canina* is a good species, and the cytologically irregular populations in Denmark are probably species hybrids. This perhaps rather extreme view is hold by many Swedish botanists.

Chromosome organization of distinct races. — Facts are accumulating showing that many of our well known Linnean species include many ecologically and genetically distinct races, which are also cytologically distinct. The wellknown cases of polyploid differences within

a species need only be mentioned. Other structural differences between two races are not so easily detected. Sometimes a close comparison of the idiograms of different races will give strong evidence, but in most cases the real truth is only brought to daylight when two races are intercrossed; the hybrid will then show structural hybridity of different kinds. If interchange between chromosome segments has happened in one race, that is, for example, if the chromosome segments *A* and *C*, *B* and *D* are joined instead of *A* and *B*, *C* and *D* in another race, a chain or ring formation will result at prophase of the hybrid. Inversion of a part of a chromosome must give fragments and duplication of a portion of a chromosome at reduction division of the hybrid, as illustrated by this example. Suppose two chromosomes *ABC* and *ACB*, where the segment *BC* is inverted, pair. The resulting daughter chromosomes may be *ABCA*, where the portion *AC* is duplicated, and the fragment *BC*, as well as *ABC* and *ACB*. From *ABCA* the segment *CA* is easily set free again (BELLING 1925, p. 263). In this way the fragments *BC* and *AC* may be formed, the relative length of which depends on the length of the originally inverted segment. Different kinds of structural dimorphismus are naturally related; each may be able to give another kind unless some special mechanism, maintaining the same structural condition, is brought in action, as in *Rhoeo discolor* (DARLINGTON 1929) and several *Oenothera* species.

Two races with practically identical genotype (taken as the sum total of genetic factors), but with the chromatic substance or »idioplasm» differently organized, may therefore give rise to all sorts of irregularities when intercrossed. Both may very well be cytologically balanced types, and be morphologically indistinguishable, yet their hybrid offspring may behave exactly as these recently discovered irregular species. It is enough that two such populations have opportunity to intercross to give rise to a population with oscillating number of chromosomes and fragments, provided that a duplication of whole chromosomes or segments does not affect the viability and only partly the fertility of the resulting offspring.

A theory accounting for cytological irregularity through intercrossing of structurally dissimilar races. — Is it too daring to asign such an origin for the Danish populations of *Viola canina*? I venture to say that it is not. Other possibilities having been discussed by CLAUSEN (1931 a, p. 83) and rejected on good grounds, he is forced to conclude that *V. canina* is not a recent segregate of the subsection and therefore not yet stabilized, but that it maintains itself through inter-

crossing between »*cytologically different types belonging to the species*»[1]. This is exactly the conclusion to which I now arrive, using the chromosomal aberrations as starting point.

We differ considerably, however, in the main conclusions we draw from this result.

1. Whereas CLAUSEN characterizes the conditions found in *Viola canina* as »rather unique», I would say that by accident only such conditions happen to have been found here as very likely exist in at least some populations of every Linnean species, excepting those too sensitive to chromosomal changes and therefore more or less monotypic. *Viola canina* is thus brought in line with most cases of »structural hybridity» (DARLINGTON 1929), and not a few such cases are known today. I need only mention the cases of ring-formation at diakinesis in *Oenothera, Rumex, Rhoeo, Tradescantia, Aucuba, Pisum* and others and the fragmentation found in *Zea, Secale, Solanum, Nicotiana, Ranunculus, Tradescantia, Ribes, Primula* and others. In some of these cases the »asymmetrical» nature of the nucleus is, no doubt, of primary nature or directly transmitted to the offspring, but in other cases the structural hybridity has probably reappeared after a cross with a cytologically different race. The best known case of chromosome configurations in intra-specific hybrids is *Datura Stramonium*, where five main chromosomal types have been found in different varieties by BLAKESLEE, BELLING and co-operators (cf. the latest report, BERGNER and BLAKESLEE 1931). Another example is recently found by me in *Ranunculus acris* L., of which wild plants having extra fragments are known from the neighbourhood of Stockholm (LANGLET 1927), Uppsala, Kalmar and from Torne Lappmark. Morphologically most of these plants belong to different races, and they grow together with externally quite similar, yet cytologically balanced plants. The conclusion is here inevitable that the structurally hybrid plants do not belong to a certain race, which has spread over a great part of Sweden, but that they are *intra-specific hybrids having their origin in the coming together of balanced races*. The Torne Lappmark type is perhaps a primary change of chromosome configuration or directly transmitted from such one, but the other cases are, no doubt, the result of crosses between one or two synanthropous races, recently spread along roadsides to cultivated areas and pasture-lands, and the natives of our *Ranunculus acris* meadows.

2. To explain the existence of cytological differences, CLAUSEN in

[1] Italics by me.

the first place mentions a polyphyletic origin of the species and crossings with another species (in the case of *Viola canina* with *V. Riviniana* and an unknown species), whereas I would identify these changes with the evolution of new subspecies and varieties.

3. »How all these cytologically different types morphologically still remain *canina* is difficult to account for», CLAUSEN says (1931 a, p. 84). I would refer to the discussion above (p. 68), where it was decided that cytologically different races may have identical equipments of genetic factors. The extra chromosomes and fragments are, no doubt, duplicates of other chromosomes.

4. As CLAUSEN considers irregular chromosome numbers as characteristic of the whole species *V. canina*, it must be pointed out that, according to the theory advocated here, balanced populations ought to exist, specially in natural habitats far away from human activity. Their occurrence in Denmark is less probable, however, considering the high degree of cultivation of the country and the fact that *V. canina* is highly hemerophilous.

In addition I want to point out the relative ease with which a cytologically balanced population of certain species apparently is infected by a cytologically dissimilar race. The reason must be that the viability of the F_1 plants is not decreased, and that they give a high proportion of gametes identical with those of both the parental races and thus have the same chance as these of surviving and further infecting the population. In inter-specific hybrids, no gametes similar to the parents are usually formed and a lower degree of fertility is the result.

Finally, as this conception of the irregular species depends on the original change as the primary cause of the structural hybridity found in intra-specific hybrids, a few words ought to be said as to its origin. However, nothing new is brought forward from CLAUSEN's or my investigations bearing on this subject, other than an indication of its minimum frequency and importance for evolution. As to its frequency, a reference may be made to *Primula*, where in a cytological study (BRUUN 1930 b) of some 250 plants of 150 species, not less than some 25 cases of »asymmetric» somatic nuclei have been met with (BRUUN 1930 a, 1931). Structural variation is certainly much more common and widespread in the vegetable kingdom than has hitherto been assumed. It is, no doubt, associated with the evolution of new varieties and subspecies and the dissimilar chromosome constitution of different po-

pulations of *Viola canina* is a strong indication in favour of this hypothesis.

I wish to acknowledge my debt to Mr. E. NORDSTRÖM, Mr. J. A. NANNFELDT, fil. lic., and Mr. N. HYLANDER, fil. stud., for their help in different ways.

SUMMARY.

1. This little study of somatic chromosomes in a wild population of pure *Viola canina* L. from the neighbourhood of Uppsala was started in consequence of CLAUSEN's interesting report (1931 a) on cytological irregularities of this species in Denmark. The Uppsala material, however, does not show any irregularities of extra chromosomes or fragments, and must therefore be cytologically better balanced than the Danish types. In all plants examined 2n is 40.

2. A theory is advanced to explain at least some cases of structural hybridity as being the result of intra-specific crossings between balanced races differing in chromosome organization. The relation of different kinds of structural changes, fragmentation, translocation, segmental interchange and inversion, is discussed, each being theoretically found able directly or indirectly to give the other types. As to the origin of the original primary change nothing is brought forward. DARLINGTON (1929, p. 281) questions »whether» (in the *Tradescantiæ*) »structural change is responsible for hybridity or hybridity for structural change». According to the theory suggested here the change must be spontaneous and primary, the structural hybridity the result of intermixing of already segregated races. In my opinion, this change is decidedly associated with evolution of new subspecies and varieties.

3. The irregularities found in *Viola canina* are recognized as an illustration of this theory. Accordingly, balanced races ought to exist, specially in unbroken districts. In Denmark, the general cultivation of the country has favoured intermixing of different races. A balanced population from near Uppsala is a confirmation of the theory.

4. Morphological similarity of cytologically different races is explained by pointing out that the nuclear variation demanded by the theory is a rearrangement of chromatic substance and may not affect the genotype.

5. Besides the wellknown important *Datura* investigations, an as yet unpublished study of chromosome fragmentation in *Ranunculus acris* is quoted in further illustration of the theory.

6. Spontaneous nuclear variation is concluded to be of common occurrence in plants.

7. Investigation of artificially obtained intra-specific hybrids is the line of further inquiry into these problems, and may throw new light upon variation and evolution.

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DISTURBED SEGREGATION RATIOS IN GALEOPSIS CAUSED BY INTRA-SPECIFIC STERILITY

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INTRODUCTION.

IN previous publications I have described and discussed cases of partial sterility in crosses between pure lines of *Galeopsis Tetrahit* L. (MÜNTZING 1929, 1930). These cases of intraspecific sterility are relatively uncomplicated and may be factorially analysed. As a rule, sterility segregation is independent of segregation in flower colour and other morphological characters. In one case, however, the cross T—B × T—C, correlation was found between segregation of flower colour and sterility.

Two factors are involved, *H* and *R*. *R* is a red factor, giving red flower colour, *rr*-plants are recessive white. The *H*-factor is an inhibitor, *Hr-* as well as *HR*-plants being dominant white. Dominant and recessive white plants may be distinguished with absolute certainty, the recessives (the T—C-type) having a distinct violet spot on the basis of the side laps, which is suppressed when the *H*-factor is present. — In the following, as in the previous paper (1930, p. 218) dominant white is called »white», recessive white is called »T—C».

The lines crossed, T—B and T—C, have the constitution *HHRR* and *hhrr* respectively. In F_2 the segregation ratio obtained was quite different from the expected 12 : 3 : 1 ratio. There was a great deficit of red plants and an excess of the T—C category (see 1930, p. 218). The F_1-hybrids are partially sterile, about half of the pollen being aborted. It was assumed that the sterility observed, as well as the disturbed segregation, was due to lethality of the recombination gametes *Hr* and *hR*. Further, this lethality was supposed to be complete in the pollen but not in the ovules, where, to a minor degree, *Hr-* and *hR*-gametes are also functional. This hypothesis was verified by an analysis of the F_2-generation. As was to be expected (see 1930, p. 220) the segregation of flower colour was not independent of the sterility segregation, the redflowered F_2-plants being semisterile, the T—C-plants

fertile, the whites in part fertile, in part sterile. — (Here and in the following »partially sterile» is abbreviated to »sterile».)

Among the T—C-plants two exceptional semisterile individuals were found. To explain this, it was assumed that the lethality of the *hR*- and *Hr*-gametes is due, not to the action of these factors *per se* but to a not absolute linkage with lethal factors. The lethal factors are called L and L_1. Gametes containing $L + L_1$ or $l + l_1$ are assumed to abort in contrast to gametes containing $L + l_1$ or $l + L_1$ (see 1930, p. 221). In regard to the two pairs of chromosomes, carrying the lethal factors and the flower colour factors, the parent lines, T—B and T—C, have the constitution $\frac{HL}{HL} + \frac{Rl_1}{Rl_1}$ and $\frac{hl}{hl} + \frac{rL_1}{rL_1}$ respectively.

In F_1 $\left(\frac{HL}{hl} + \frac{Rl_1}{rL_1}\right)$ most of the vital gametes have the constitution $hl + rL_1$ and $HL + Rl_1$. To a minor degree other types of gametes are also functional. These belong to two different categories: 1) Such types which arise by crossing over in one or the other of the chromosome pairs or in both pairs simultaneously. These types are represented to an equal degree in both pollen and ovules. 2) Gametes which are lethal in the pollen but to some degree functional in the ovules. Consequently, the following 16 types of gametes may be formed and function (table 1).

TABLE 1. *Types of F_1-gametes.*

	No.	Vital gametes	No.	Pollen-lethal gametes
Non-crossover	1	$HL + Rl_1$	9	$HL + rL_1$
	2	$hl + rL_1$	10	$hl + Rl_1$
Crossover in one chromosome pair	3	$Hl + rL_1$	11	$Hl + Rl_1$
	4	$hL + Rl_1$	12	$hL + rL_1$
	5	$HL + rl_1$	13	$HL + RL_1$
	6	$hl + RL_1$	14	$hl + rl_1$
Crossover in both pairs	7	$hL + rl_1$	15	$hL + RL_1$
	8	$Hl + RL_1$	16	$Hl + rl_1$

The relative frequency of these gametes depends in part on the linkage values, in part on the relative viability of those female gametes that have a pollenlethal constitution.

In the report of the F_2-results it was concluded (1930, p. 221) that two exceptional semisterile T—C-plants must have the constitution

$\frac{hL}{hl} + \frac{rl_1}{rL_1}$. Therefore, they ought to be the result of a union between one normal $hl + rL_1$-gamete and another gamete $hL + rl_1$. Gametes of the latter kind would result from a simultaneous crossover in both chromosome pairs. — However, another and more probable origin of semisterile T—C-plants was overlooked. Gametes resulting from crossover in one pair, $hl + rl_1$ and $hL + rL_1$, are lethal in the pollen but to some degree functional in the ovules. Combined with ordinary $hl + rL_1$-gametes the result will be $\frac{hL}{hl} + \frac{rL_1}{rL_1}$ or $\frac{hl}{hl} + \frac{rl_1}{rL_1}$. These combinations will give T—C-plants, which are semisterile in the pollen.

In order further to test the theory, given as an explanation of the F_2-results, F_3- and F_4-generations were raised and analysed as to segregation of flower colour and its connection with the sterility conditions. The present paper gives the F_3- and F_4-results and some additional data from another cross.

THE F_3-GENERATION.

1. PROGENIES OF RED F_2-PLANTS.

According to the theory, the redflowered F_2-plants have the constitution $\frac{hr}{hR}$. In the pollen hR is completely lethal (excepting the results of crossing-over between the flower colour and lethal factors), in the ovules this combination is partially lethal (»sublethal»). Therefore, only one kind of male gametes (hr) are vital. On the female side most functional gametes have the same constitution, but also hR-gametes may function to some degree. The result in the progeny must be a majority of recessive T—C-plants and a minority of redflowered individuals. This result was in fact obtained (table 2, nos. 1—5).

Five progenies [1] of redflowered and partially sterile F_2-plants all consisted of a higher number of recessive than dominant individuals. A total of 51 red and 132 T—C-plants was obtained. Thus, *instead of segregation in 3 red: 1 T—C, the ratio is almost completely turned into the opposite direction, giving about 3 recessive : 1 dominant.* This is in complete agreement with the explanation given for the F_2-results.

The theory might be further verified or disproved by investigations of the pollen fertility. According to the theory, homozygous recessive plants $\left(\frac{hr}{hr}\right)$ should be generally fertile, the heterozygous redflowered

[1] All progenies described in this paper are the result of controlled selfing.

TABLE 2. *Segregation ratios in progenies of redflowered F_2- and F_3-plants.*

Table number	Generation	Field number	red	T—C	n	Pollen percentage of the mother plant	Per cent red
1	F_3	1930—19	5	22	27	46	—
2	»	—20	7	27	34	51	—
3	»	—21	25	43	68	54	—
4	»	—22	2	13	15	38	—
5	»	—23	12	27	39	56	—
1—5	»	F_3, total	51	132	183	49 (average)	$27{,}9 \pm 3{,}3$
6	F_4	1931—20	10	21	31	50	—
7	»	—21	6	21	27	59	—
8	»	—22	2	20	22	44	—
9	»	—24	9	26	35	49	—
6—9	»		27	88	115	51 (average)	$23{,}5 \pm 3{,}9$
10	»	1931—25	10	18	28	70	—
11	»	—26	11	24	35	74	—
12	»	—27	17	13	30	63	—
13	»	—28	12	23	35	67	—
14	»	—23	7	17	24	62	—
10—14	»		57	95	152	67 (average)	$37{,}5 \pm 3{,}9$
15	»	1931—29	27	14	41	94	—
16	»	—30	25	7	32	93	—
17	»	—31	10	6	16	92	—
18	»	—32	11	5	16	95	—
19	»	—33	20	7	27	98	—
20	»	—35	20	6	26	98	—
15—20	»		113	45	158	95 (average)	$71{,}5 \pm 3{,}6$
21	»	1931—34	23	6	29	64	79

plants should be semisterile just as in F_2. In analogy to F_2 a small percentage of exceptions (sterile recessives and fertile dominants) should also be obtained due to crossing-over between lethal factors and flower colour factors.

In all plants of the five F_3-families under discussion the percentage of good pollen was calculated in the usual way. The result is given in table 3, nos. 1—5.

Obviously the sterility conditions as well as the disturbed segrega-

TABLE 3. *Pollen fertility in F_3.*

Table number	Field number and type of flower colour	Good pollen 30—35	35—40	40—45	45—50	50—55	55—60	60—65	65—70	70—75	75—80	80—85	85—90	90—95	95—100 %	n	Flower colour of the mother plant	Pollen percentage of the mother plant
1 a	1930—19, red	—	—	—	—	2	—	—	—	1	—	—	—	1	1	5	red	46
2 a	—20, »	—	—	1	3	1	2	—	—	—	—	—	—	—	—	7	»	51
3 a	—21, »	—	—	1	4	2	5	7	—	3	—	—	—	2	1	25	»	54
4 a	—22, »	—	—	—	2	—	—	—	—	—	—	—	—	—	—	2	»	38
5 a	—23, »	1	—	—	2	3	3	—	—	—	—	—	—	1	2	12	»	56
1 a—5 a	red, total	1	—	2	11	8	10	7	—	4	—	—	—	4	4	51	»	49 (average)
1 b	1930—19, T—C	—	—	—	—	—	1	—	—	1	1	1	2	5	11	22	»	46
2 b	—20, »	—	—	—	—	1	—	—	1	1	2	—	—	5	17	27	»	51
3 b	—21, »	—	—	—	1	—	—	—	—	1	—	1	—	6	34	43	»	54
4 b	—22, »	—	—	—	1	—	1	—	—	—	1	—	—	5	5	13	»	38
5 b	—23, »	—	—	1	—	1	—	—	—	—	—	—	—	3	22	27	»	56
1 b—5 b	T—C, total	—	—	1	2	2	2	—	1	3	4	2	2	24	89	132	»	49 (average)
6	1930—24, T—C	—	—	—	—	—	—	—	—	—	—	—	3	8	27	38	T—C	95—100
7	—25, »	—	—	—	—	—	—	—	—	—	—	—	—	3	13	16	»	93
8	—26, »	—	—	—	—	—	—	—	—	—	—	—	2	6	26	34	»	95—100
9	—27, »	—	—	—	—	—	1	—	1	2	3	—	3	8	4	22	»	52
10 a	—28, »	—	—	—	—	—	—	—	—	—	—	—	2	2	4	8	white	95—100
10 b	» , white	—	—	—	—	—	—	—	—	—	—	1	2	5	16	24	»	»
11	—29, »	—	—	—	2	2	—	—	2	8	2	1	5	6	16	44	»	71
12	—30, white, red, T-C	—	—	—	—	—	—	1	—	—	—	—	1	2	29	33	»	95—100
13	—31,	—	—	—	4	2	1	1	2	—	—	1	2	3	7	23	»	36

tion ratios are in perfect agreement with the theory. Among 51 red-flowered plants 43 are clearly sterile, the remaining 8 are fertile. On the contrary, out of 132 white-flowered plants at least 113 belong to the fertile category, the rest being more or less sterile.

2. PROGENIES OF F_2-PLANTS OF THE T—C-TYPE.

Four F_3-families were raised from F_2-plants of the T—C-type. In all, 112 individuals were obtained, all of which had the same type of flower colour as their mother plants. Three of the progenies were the descendants of fertile F_2-plants and consisted exclusively of fertile or practically fertile individuals (table 3, nos. 6—8), one family was raised from an exceptional, partially sterile F_2-plant. In contrast to the fertile progenies the last-mentioned family (table 3, no. 9) consisted of both fertile and sterile individuals, which is in accordance with expectation.

3. PROGENIES OF WHITE F_2-PLANTS.

Two fertile and two partially sterile, white F_2-plants were used as mother plants for F_3-progenies (table 3, nos. 10—13).

A. FERTILITY VARIATION.

a) PROGENIES OF FERTILE MOTHER PLANTS.

Family 1931—28 consisted of 32 plants. The mother plant had 95—100 per cent good pollen. In this progeny 27 plants had at least 90 per cent good pollen. The remaining 5 plants had a pollen percentage ranging from 80 to 90 per cent (table 3, no. 10). Most probably the slight sterility in these plants was due to modificatory disturbances.

Progeny 1931—30 consisted of 33 plants of which 32 were fertile like the mother plant, one plant, however, was partially sterile contrary to expectation (table 3, no. 12). An F_4-progeny was raised from this exceptional plant (see below, p. 89).

b) PROGENIES OF STERILE MOTHER PLANTS.

One F_2-plant had on an average 36 per cent good pollen. The progeny ($n = 23$) consisted of 13 fertile and 10 approximately semi-sterile individuals (table 3, no. 13). Another F_3-family (1931—29) from a mother plant having 71 per cent good pollen showed another type of sterility variation (table 3, no. 11). Among 44 plants 4 were semi-sterile, 12—13 had about the same degree of sterility as the mother plant and the remaining plants were fertile. This reminds of the type of sterility variation found in the »quartersterile» crosses (cf. 1930, p. 226). Consequently, though in the cross now discussed the partially

sterile individuals generally show abortion of about half of the pollen, quartersterile individuals seem to arise which in the following generation give a different type of sterility variation.

B. SEGREGATION RATIOS.

The two progenies of sterile white mother plants were constant in respect of flower colour, the two progenies of fertile mother plants gave segregation. Family 1931—28 consisted of 24 white and 8 T—C-plants, family 1931—30 gave the ratio 27 white : 4 red : 2 T—C. As in these cases mother plants as well as progeny were fertile, the values found probably correspond to the segregation ratios 3 : 1 and 12 : 3 : 1 respectively (cf. below p. 86).

According to the theory most fertile white-flowered F_2-plants should be homozygous *HHRR,* being the result of a union between vital *HR*-gametes. A smaller group of heterozygous but fertile plants might arise from the union of normal and crossover gametes, or in rare cases from the union of two crossover gametes. Only progenies of two fertile white F_2-plants were raised, but it is surprising to find that both of them were heterozygous. According to the segregation ratios the genotypical constitution of the mother plants was *Hhrr* and *HhRr* respectively. — Consequently it seems safe to conclude that a higher proportion of white flowered and heterozygous, but fertile F_2-plants arise than can be explained, as the result of crossing over between the flower colour factors and lethal factors.

Some other unknown cause must be in part responsible. It may be remembered that in several crosses previously described (1929, p. 308; 1930, p. 223) progenies segregating in fertile and sterile, showed a relative excess of fertile individuals. This was also the case in the present cross T—B × T—C, at least concerning the white F_2-plants. More than twice as many sterile as fertile plants should be expected (see the scheme 1930, p. 219) but in fact more fertile than sterile plants were obtained. If e. g. selective zygotic viability or some other cause favours the fertile category, this may at least in part also explain the unexpected frequency of heterozygous but fertile, white F_2-plants.

THE F_4-GENERATION.

Though in all main respects the F_3-analysis confirmed the explanation given for the F_2-results, some obscure points remained to be further investigated. Therefore, from 26 F_3-plants F_4-progenies were raised, comprising a total of 721 plants.

1. PROGENIES OF RED F_3-PLANTS.

A. PROGENIES OF STERILE RED.

a) SEGREGATION RATIOS.

From 9 F_3-plants a total of 267 daughter plants was obtained. As was to be expected these progenies showed the same type of segregation as the corresponding F_3-families, viz. instead of 3 : 1 segregation a great excess of the recessive T—C-plants and a minority of the dominant red plants. In all 84 red: 183 T—C-types were obtained (table 2, nos. 6—14).

However, different families seem to give somewhat different proportions of red: T—C. As to the degree of sterility there was some variation among the mother plants, the percentage of good pollen ranging from 44—74. Now the most sterile mother plants seem to give a lower proportion of red flowered descendants than the others. Four mother plants having from 44—59 per cent good pollen, gave in the following generation on an average $23{,}5 \pm 3{,}9$ per cent redflowered plants (table 2, nos. 6—9). The other five families which were raised from more fertile mother plants (the pollen percentage = 62—74) gave an average of $37{,}5 \pm 3{,}9$ per cent (table 2, nos. 10—14). The difference $37{,}5 - 23{,}5 = 14{,}0 \pm 5{,}5$ is probably significant, the odds being 81 : 1.

If in a plant of the constitution $\frac{hl}{hl} + \frac{rL_1}{Rl_1}$ all $hl + Rl_1$-gametes, male as well as female, are eliminated, the progeny will consist exclusively of recessive T—C-plants. As a minority of red plants is also obtained, and since on an average 50 per cent of the pollen is aborted, it is probable that ovules carrying the red-factor are to some extent functional. If more than 50 per cent of the pollen is good, pollen grains carrying an otherwise lethal constitution, are at least morphologically normal. They may perhaps also be functional but probably they will not be able to compete with the other vital class of pollen grains. More likely the increased proportion of red plants is due to an increased ability of ovules, carrying the red-factor, to function. The higher male and female fertility may be due to environmental factors or possibly to genetic modifiers.

b) FERTILITY VARIATION.

As in F_3 the progenies of red sterile chiefly consisted of fertile T—C and sterile, redflowered plants. A minority of sterile T—C and fertile red was also obtained. The fertility variation is given in table 4.

In regard of flower colour segregation, progenies of mother plants

TABLE 4. *Pollen fertility in F_4-progenies of redflowered, partially sterile F_3-plants.*

Table number	Field number and type of flower colour	Good pollen 30—35—40—45—50—55—60—65—70—75—80—85—90—95—100 %															n	Pollen percentage of the mother plant
1 a	1931—20, red	—	—	—	—	2	2	1	1	—	1	—	1	2	—		10	50
2 a	—21, »	—	—	1	1	—	—	—	—	—	—	—	—	1	3		6	59
3 a	—22, »	—	—	—	—	1	—	—	—	—	—	—	—	1	—		2	44
4 a	—24, »	—	—	—	2	2	3	—	—	—	—	—	—	—	2		9	49
1 a—4 a	total, »	—	—	1	3	5	5	1	1	—	1	—	1	4	5		27	51 (average)
5 a	1931—23, red	—	—	—	1	1	1	—	—	—	—	1	—	1	2		7	62
6 a	—25, »	—	—	—	1	6	—	1	1	1	—	—	—	—	—		10	70
7 a	—26, »	—	—	—	1	3	—	2	—	2	1	1	—	—	1		11	74
8 a	—27, »	—	—	1	1	—	3	2	—	—	1	—	—	3	6		17	63
9 a	—28, »	1	—	—	1	—	1	1	—	3	1	1	—	2	1		12	67
5 a—9 a	total, red	1	—	1	5	10	5	6	1	6	3	3	—	6	10		57	67 (average)
1 a—9 a	total, red	1	—	2	8	15	10	7	2	6	4	3	1	10	15		84	
1 b	1931—20, T—C	—	—	—	—	—	1	—	—	—	—	1	3	11	5		21	50
2 b	—21, »	—	—	—	—	—	1	—	—	—	—	—	4	3	12		20	59
3 b	—22, »	—	—	—	—	—	—	—	1	—	2	—	2	4	9		18	44
4 b	—24, »	—	—	—	—	—	—	—	—	—	—	—	—	—	25		25	49
5 b	—23, »	—	—	—	—	—	1	—	1	—	1	2	1	—	10		16	62
6 b	—25, »	—	—	—	1	—	—	—	—	—	—	—	1	4	12		18	70
7 b	—26, »	—	—	—	—	—	—	—	—	—	—	1	5	9	9		24	74
8 b	—27, »	—	—	—	—	—	—	—	—	1	—	—	—	2	10		13	63
9 b	—28, »	—	—	—	—	—	—	—	—	1	—	—	—	1	20		22	67
1 b—9 b	total, T—C	—	—	—	1	—	3	—	2	2	3	4	16	34	112		177	60 (average)

having 62—74 per cent good pollen gave a higher percentage of red-flowered descendants than mother plants being more sterile. It may be mentioned that a difference in the relative frequency of red sterile and red fertile was also observed, according to the type of mother plant. The more sterile mother plants (table 4, nos. 1—4) gave in F_4 63 per cent sterile and 37 per cent fertile red, the other category of mother plants (table 4, nos. 5—9) gave 72 per cent sterile and 28 per cent fertile red. Though the difference is not significant, it supports the view that in relatively fertile mother plants a higher proportion of ovules, carrying the pollen lethal constitution, are functional.

When the relative frequency of red sterile : red fertile is compared, it is striking that the proportion of fertile red seems to increase in successive generations. In F_2 the 21 redflowered plants obtained were all partially sterile, in F_3 43 plants were sterile, 8 fertile ($15{,}7 \pm 5{,}1$ % fertile), in F_4 the proportion was 58 sterile : 26 fertile ($32{,}1 \pm 5{,}1$ % fertile).

The difference between F_2 on the one hand, and F_3 and F_4 on the other, may be due to the fact that red F_2-plants are the descendants of F_1-plants having the constitution $\frac{HL}{hl} + \frac{Rl_1}{rL_1}$, whereas red F_3- and F_4-plants generally arise from plants of the constitution $\frac{hl}{hl} + \frac{rL_1}{Rl_1}$. Theoretically red, semisterile F_2-plants may also have the constitution $\frac{hl}{hL} + \frac{rL_1}{RL_1}$. However, as $hL + RL_1$-gametes can only be formed by means of simultaneous crossover in both chromosome pairs (cf. table 1) and only part of the female gametes, carrying the pollen lethal factors, function, $hL + RL_1$-gametes must be very rare. Therefore, practically all red, semisterile F_2-plants have the constitution $\frac{hl}{hl} + \frac{rL_1}{Rl_1}$. Such plants form functional gametes of the following types:

	non-crossover	crossover
male gametes:	$hl + rL_1$	$hl + RL_1$
female gametes:	$hl + rL_1$	$hl + RL_1$
	$(hl + Rl_1)$	$(hl + rl_1)$

The pollenlethal combinations which function to some degree in the ovules are put in brackets.

The eight possible combinations between these four types of gametes will give the following result (table 5).

Now, in F_2 red sterile plants may be formed in two ways, *partly*

due to functioning of female gametes having pollenlethal constitution, *partly* due to the formation of crossover gametes. As may be easily calculated from the types of F_1-gametes given above (table 1) red sterile may e. g. result from the union of one normal gamete $hl + rL_1$ and one single crossover gamete $hL + Rl_1$.

In F_3 and F_4 the situation is different. As will be seen from table 5, red sterile plants can here only arise in the first way, viz. by functioning of ovules carrying pollen lethals. The combinations normal $\times$ single crossover give here only red fertile. This may explain the higher percentage of red fertile in F_3 and F_4 in comparison with F_2.

TABLE 5. *Possible combinations in the progeny of red, semi-sterile.*

	$hl + rL_1$	$hl + RL_1$	
$hl + rL_1$	1) $\frac{hl + rL_1}{hl + rL_1}$	2) $\frac{hl + RL_1}{hl + rL_1}$	1) = T—C, fertile 2) = red, »
$hl + RL_1$	3) $\frac{hl + rL_1}{hl + RL_1}$	4) $\frac{hl + RL_1}{hl + RL_1}$	3) = » , » 4) = » , »
$(hl + Rl_1)$	5) $\frac{hl + rL_1}{hl + Rl_1}$	6) $\frac{hl + RL_1}{hl + Rl_1}$	5) = » , sterile 6) = » , »
$(hl + rl_1)$	7) $\frac{hl + rL_1}{hl + rl_1}$	8) $\frac{hl + RL_1}{hl + rl_1}$	7) = T—C, sterile 8) = red, »

However, when F_3 and F_4 are compared it will be seen that the percentage of red fertile is not the same but higher in F_4 than in F_3, the values being $32{,}1 \pm 5{,}1$ % and $15{,}7 \pm 5{,}1$ % respectively. The difference is $16{,}4 \pm 7{,}2$ and $D/m_D = 2{,}3$. The odds that this difference is significant are 47 : 1. At present no sure explanation can be given of this increase in fertility.

c) ESTIMATION OF THE AMOUNT OF CROSSING-OVER BETWEEN FLOWER COLOUR AND LETHAL FACTORS.

Theoretically the amount of crossing over between the *R*- (rsp. *r*-) factor and the lethal factors L_1—l_1 may be estimated by comparing the relative frequency of different categories in the progenies from red semi-sterile. According to the scheme (table 5), combination no. 1 gives the category T—C fertile and combinations 2—4 red fertile. If the frequencies of non-crossover- and crossover-gametes are a and b resp.,

the number of T—C fertile = n and of red fertile = m, the following equations will be obtained: $a^2 = n$ and $2ab + b^2 = m$. In F_3 the values 115 T—C and 8 red were obtained, plants with 85—100 % good pollen being regarded as fertile. In F_4 the corresponding numbers were 162 and 26. This gives the a/b values 29 and 13 resp. That is, in the first case about 3 per cent crossover gametes, in the second case about 7 per cent.

Another way of estimating the amount of crossing-over should be to compare the frequency of categories 5 and 7 of table 5. Category 5 (red sterile) is the result of a union between a vital male non-crossover gamete $hl + rL_1$ and a female »sublethal» $hl + Rl_1$-gamete. Combination 6 of the scheme also gives red sterile but must be very rare and may be disregarded, being a combination between a male crossover gamete and a sublethal female gamete. Combination 7 is the only combination giving T—C sterile and results from the union of one normal gamete $hl + rL_1$ and one crossover gamete $hl + rl_1$. If the viability of the two kinds of female gametes, non-crossovers ($hl + Rl_1$) and crossovers ($hl + rl_1$) is the same, the relative frequency of red sterile and T—C sterile should give an approximate value of the amount of crossover. If, as previously, the limit between fertility and sterility is placed at 85 per cent good pollen, the values obtained in F_3 are 43 red sterile : 17 T—C sterile. In F_4 the corresponding ratio 58 : 15 was obtained. This would give the crossover values 28 and 21 respectively. Evidently these values are in poor agreement with the values 3 and 7 obtained by the previous method.

However, this is most probably due to the fact that sometimes it is impossible to draw a sharp line between the two categories fertile and partially sterile. When a large number of genotypically fertile individuals are investigated, some individuals will show some degree of partial sterility due to modifying causes. This has been observed in pure lines (cf. table 8, p. 90) and other progenies from fertile mother plants, especially at the end of the flowering period. In this respect table 6 (p. 87) ist instructive. In the progenies from fertile mother plants the fertility curve is skew. The maximum is generally in the highest fertility class and the lower classes show a continuous decrease in number of individuals. But some plants may have as much as 30—40 per cent bad pollen. In the F_3- and F_4-progenies of red semisterile the majority of the plants belong to the category T—C fertile. A small number are T—C sterile. If the limit between fertility and sterility is placed at 85 per cent, some genotypically fertile plants will

show less than 85 per cent good pollen and hence the category T—C sterile will be falsely increased. This will give a false relation red sterile : T—C sterile, because the sterile, red plants will not get a similar addition of pseudo-sterile plants. This is due to the fact that the category red fertile is very small in relation to the category red sterile in contrast to the relation between T—C fertile and T—C sterile. Therefore, calculations of the amount of crossing-over based upon comparison of the relative number of sterile red and sterile T—C will give a too high crossover value. Comparison of the number of fertile T—C and fertile red on the other hand will give more reliable figures. Consequently, the crossover value under discussion may be roughly estimated to be 5—10 per cent.

d) ESTIMATION OF THE RELATIVE FREQUENCY OF VITAL AND SUBLETHAL FEMALE GAMETES.

By sublethal female gametes are understood the types having a pollenlethal genotypical constitution ($L + L_1$ or $l + l_1$). As previously shown these combinations function to a certain extent in the ovules. The majority of the female gametes, however, have the vital constitution $L + l_1$ or $l + L_1$. The relative number of functioning vital and sublethal female gametes may be estimated by comparing the numbers of fertile and sterile descendants from red sterile mother plants. As is evident from table 5, all sterile individuals (combinations 5—8) result from the union of sublethal female and vital, male gametes, all fertile plants (combinations 1—4) from the union of vital female and vital male gametes.

The number of fertile and sterile individuals in F_3 and F_4 (descendants of red sterile) may be taken from tables 3 and 4. If the limit between fertile and sterile is placed at 85 %, the numbers obtained are, in F_3, 123 fertile : 60 sterile, and in F_4 188 fertile : 73 sterile. Consequently, the percentage of functioning sublethal female gametes in F_2 and F_3 will be 33 and 28 respectively. However, these values cannot be very accurate. Firstly, modificatory sterility may tend to increase the percentage (compare the preceding paragraph). Secondly, if there is a zygotic selection, favouring the fertile combinations (comp. p. 79) the percentage values obtained are *minimum*values.

However, if the pollenlethal combinations were also lethal in the ovules, the semisterile red plants would give only fertile descendants. If, on the other hand, *all* kinds of ovules are equally viable and if no zygotic selection occurs, fertile and sterile individuals would be obtained in equal number. As a majority of fertile plants are actually obtained,

this must be due, either to a higher proportion of functioning, non-lethal ovules or to zygotic selection or to both phenomena. This will be further discussed below (p. 95).

B. PROGENIES OF FERTILE RED.

a) SEGREGATION RATIOS.

The red, sterile F_2-plants gave in F_3 a clear delimitation in 8 fertile and 43 partially sterile individuals (table 3). As previously discussed (see table 5) the fertile red plants must in most cases result from the union of one crossover gamete and one normal gamete (combinations 2 and 3). Only in very rare cases two crossover gametes may meet and form homozygous red plants (combination 4).

Consequently, most red fertile plants should in next generation give segregation in red and T—C. As the mother plants are fertile and therefore no selective elimination of gametes due to sterility can occur, these plants, in contrast to their sterile mother plants, should give normal monohybrid segregation in 3 red : 1 T—C-type. This also proved to be the case. From 6 of the fertile red F_3-plants a total of 158 descendants were raised, of which 113 (that is $71{,}5 \pm 3{,}6$ per cent) were red, 45 of the T—C-type (table 2). These 6 families (table 2, nos. 15—20) gave all segregation ratios, which evidently correspond to normal monohybrid segregation. They contrast strikingly to the progenies of red sterile plants (table 2, nos. 1—14), where the 3 : 1 segregation is almost changed to a 1 : 3 ratio.

In this connection it may be remembered that two F_3-families described above (p. 79) which were raised from white, fertile F_2-plants gave segregations most probably corresponding to the ratios 3 : 1 and 12 : 3 : 1.

Thus, *when fertility is normal, segregation is also normal, when partial sterility occurs segregation is very much disturbed.* In combination with the previous results this agreement between prediction and actual observation definitely proves that fertility conditions and segregation ratios are correlated in this cross. And it seems quite safe to conclude that partial sterility here is the *cause* of abnormal segregation ratios.

b) FERTILITY VARIATION.

The mother plants of the six progenies of red fertile had from 92 to 98 per cent good pollen. Among the daughter plants there was some variation (table 6, nos. 1—6), a few individuals showing as much as 30—35 per cent abortion of pollen. However, the highest fertility

TABLE 6. *Pollen fertility in progenies of fertile F_3-plants.*

Table number	Field number and type of flower colour	Good pollen 60—65—70—75—80—85—90—95—100 %	n	Flower colour of the mother plant	Pollen percentage of the mother plant
1 a	1931—29, red	— — — — 1 3 5 18	27	red	94
2 a	—30, »	— — — — — 4 3 15	22	»	93
3 a	—31, »	— 2 — 1 — 3 3 —	9	»	92
4 a	—32, »	— — 1 3 — 1 6 —	11	»	95
5 a	—33, »	— — — — 2 6 3 5	16	»	98
6 a	—35, »	— — — 1 1 4 6 4	16	»	98
1 a—6 a	total, »	— 2 1 5 4 21 26 42	101	»	95 (average)
1 b	1931—29, T—C	— — — — 1 1 2 10	14	»	94
2 b	—30, »	— — — — 1 2 1 3	7	»	93
3 b	—31, »	— — — — — 2 4 —	6	»	92
4 b	—32, »	— — — 1 — 1 3 —	5	»	95
5 b	—33, »	— — — — 1 3 — 1	5	»	98
6 b	—35, »	— — — — — 2 1 3	6	»	98
1 b—6 b	total, »	— — — 1 3 11 11 17	43	»	95 (average)
7	1931—42, »	1 — — 3 2 1 4 2	13	T—C	92
8	—43, »	— — 1 1 8 10 6 2	28	»	96
7—8	total, »	1 — 1 4 10 11 10 4	41	»	—

TABLE 7. *Pollen fertility in F_4-progenies of different types of sterile F_3-plants.*

Table number	Field number and type of flower colour	Good pollen 40—45—50—55—60—65—70—75—80—85—90—95—100 %													n	Flower colour of the mother plant	Pollen percentage of the mother plant
1	1931—36, T—C.....	1	1	1	2	1	—	2	—	6	9	6	12		41	T—C	57
2	—37, »	1	—	—	—	—	—	1	—	—	2	—	9		13	»	52
3	—38, »	1	—	—	5	1	1	—	1	1	1	5	12		28	»	58
1—3	total, »	3	1	1	7	2	1	3	1	7	12	11	33		82	»	56 (average)
4	1931—39, »	—	—	—	—	—	—	—	1	—	5	14	15		35	»	81
5	—40, »	—	—	—	—	5	4	1	5	7	5	3	1		31	»	75
6	—41, »	—	1	—	2	2	—	—	1	3	2	3	1		15	»	78
7	1931—44, white.....	—	—	—	—	1	1	4	4	5	3	8	8		34	white	46
8	—46, »	—	—	—	—	1	5	6	8	7	9	3	1		40	»	75
9 a	1931—34, red	—	1	—	1	3	2	2	—	1	4	1	6		21	red	59
9 b	» », T—C.....	—	—	—	—	—	1	—	—	1	1	1	2		6	»	»

class is the greatest one and, as previously argumented, the slight amount of partial sterility observed must be ascribed to environmental influences, not to a lethal genotypical constitution of the pollen grains.

2. PROGENIES OF RECESSIVE WHITE F_3-PLANTS (THE T—C-TYPE).

All progenies of F_3-plants of the recessive T—C-type were constant in flower colour type. As to fertility some progenies were obtained from fertile, others from partially sterile mother plants.

A. PROGENIES OF STERILE T—C.

Three F_3-plants with a pollen percentage of 57, 52 and 58 respectively gave in next generation progenies, comprising a total of 82 individuals (table 7, nos. 1—3). Of these plants 56 had from 85 to 100 per cent good pollen, the remaining 26 were partially sterile, the percentage of good pollen varying from 40 to 85 with a possible maximum at 55—60. This is in agreement with expectation, since sterile T—C-plants of the type $\frac{hl}{hl} + \frac{rL_1}{rl_1}$ should be expected to give a majority of fertile and a minority of sterile descendants, the latter ones due to partial functioning of female $hl + rl_1$-gametes.

The proportion of fertile to sterile plants in these progenies may also be used for calculation of the relative frequency of vital and sublethal female gametes. The same argumentation as given above for the progenies of red sterile, holds good also for the present case. If the values of the three F_4-families and one F_3-family of the same type (table 3, no. 9) are added, the relation of fertile to sterile plants will be 71 : 33. According to this, 32 per cent of the functioning female gametes carry the pollen lethal constitution which is in agreement with the previous values 33 and 28 (see p. 85).

B. PROGENIES OF FERTILE T—C.

In addition to the fertile F_3-progenies of fertile F_2-plants two F_4-progenies of the same kind were raised. These progenies (table 6, nos. 7—8) were investigated at the end of the flowering period, and probably therefore they show some variation in fertility. Most probably, however, they are genotypically of the same kind as the F_3-progenies, where no plants have less than 85 per cent good pollen.

3. SOME EXCEPTIONAL PROGENIES.

A) As already mentioned (p. 78) in one F_3-progeny (table 3, no. 12) there appeared an exceptional plant which was partially sterile in con-

trast to the mother plant and 32 sister plants. The plant in question was redflowered and gave in F_4 a probably monohybrid segregation in 23 red : 6 T—C (table 2, no. 21). The fertility of these plants was investigated (table 7, no. 9). Some plants were fertile, others more or less sterile. As to fertility there was no evident difference betweeen the red and T—C-plants. Thus, in this case the sterility observed does not affect the segregation ratio. This may be connected with the fact that the mother plant arose as an exception in an otherwise fertile progeny of a fertile mother plant. No sure explanation of the case can be given at present.

TABLE 8. *Pollen fertility in pure lines of Galeopsis Tetrahit and bifida.*

Table no.	Line and year	Good pollen 65—70—75—80—85—90—95—100 %							n
1	T—A, 1930	—	—	—	—	—	—	4	4
2	T—B, »	—	—	—	—	—	—	4	4
3	» , 1931	—	—	—	—	—	—	5	5
4	T—C, »	—	—	—	1	1	5	3	10
5	T—D, 1930	—	—	1	—	—	—	2	3
6	» , 1931	—	—	—	—	—	—	8	8
7	T—E, 1930	—	—	—	—	—	—	5	5
8	T—F, »	—	—	—	—	—	—	5	5
9	T—G, »	—	—	1	1	5	4	5	16
10	T—L, »	—	—	1	—	1	1	2	5
11	T—M, »	—	—	—	—	—	1	4	5
12	T—N, »	—	—	—	—	—	—	4	4
13	» , 1931	—	—	—	—	—	—	10	10
14	»Yellow *Tetrahit*», 1930	1	—	—	—	1	—	4	6
15	T—X, 1930	—	—	—	—	—	1	4	5
16	B—A, 1931	—	—	—	—	—	—	10	10
17	B—B, 1930	—	—	—	—	—	—	5	5
18	B—E, 1931	—	—	—	—	—	2	9	11
19	B—F, »	—	—	1	—	—	1	8	10
1—19	total	1	—	4	2	8	15	101	131

B) Besides the three F_4-progenies of semisterile T—C-plants three other progenies of T—C-plants were raised (table 7, nos. 4—6). In the latter case the mother plants had 75, 78 and 81 per cent good pollen respectively. These families were grown to see whether mother plants having about $^1/_4$ of their pollen aborted, would give the same kind of variation in next generation as the F_3-family previously described. This

family seemed to show the same variation as in »quartersterile» crosses. However, the present progenies behaved differently. In progeny no. 4, 34 out of 35 plants had at least 85 per cent good pollen. Therefore, these plants must all be regarded as genotypically fertile, and the sterility of the mother plant (pollen percentage = 81) as being caused solely by environment. Progeny no. 6, on the contrary, consisted of fertile as well as of clearly sterile individuals. The type of variation seems to be the same as in the progenies of typically semisterile plants. Therefore, though the pollen percentage of the mother plant happened to get a rather high value this plant was probably genotypically semisterile.

Progeny no. 5 represents a third type. There is no clear delimitation in fertile and sterile plants, and most individuals have about the same amount of bad pollen as the mother plant.

No sure explanation of the sterility in this progeny can be given at present. However, it was observed that in some of the plants the anthers were in part badly developed. Then the partial sterility in this family may be caused by somatic disturbances.

C) Two progenies of dominant white F_3-plants, having the pollen percentage 46 and 75 respectively, showed the same type of fertility variation as the T—C-family just discussed (table 7, nos. 7—8). Probably the cause of the disturbances in pollen development is the same in all three cases. Evidently it has nothing to do with the lethal factors, controlling fertility and sterility in all other progenies investigated.

CORRELATION BETWEEN FLOWER COLOUR AND SPEED OF DEVELOPMENT.

In F_3 it was observed that the redflowered plants in progenies segregating in red : T—C, started flowering later than the recessive white T—C-plants. Four countings were made (table 9). The percentage of red plants was at the first counting 20,4, at the second 24,0, at the third 25,2 and at the fourth 27,9, thus showing a continuous increase. When comparing the percentage of fertile and sterile plants at each counting, irrespective of flower colour, a still more obvious increase in the percentage of sterile plants took place. The values at the first and last counting were $21{,}4 \pm 4{,}0$ and $32{,}8 \pm 3{,}5$ respectively, the difference being $11{,}4 \pm 5{,}3$ ($D/m_D = 2{,}2$). It may be remembered that in the F_3-progenies most sterile plants are redflowered, most fertile ones of the T—C-type. Then the question must be raised, whether the sterile plants are late in flowering because they are generally red-

TABLE 9. *Speed of somatic development in F_3 and F_4.*

	F_3-progenies of sterile mother plants			F_4-progenies of sterile mother plants			F_4-progenies of fertile mother plants		
	n	% red	% sterile	n	% red	% sterile	n	% red	% sterile
1st counting	103	20,4	21,4 ± 4,0	116	4,3 ± 1,8	—	76	60,5 ± 5,6	—
2nd »	154	24,0	26,0	183	18,6	—	125	65,6	—
3rd »	163	25,2	28,8	230	26,1	—	145	69,0	—
4th »	183	27,9	32,8 ± 3,5	267	31,5±2,9	—	158	71,5 ± 3,6	—

flowered, or if, inversely, the redflowered ones are late, because they are generally sterile? The F_3 data alone are not sufficient to settle the question, but from the fact that the percentage of sterile plants shows a greater increase than the percentage of redflowered ones, it may be surmised that sterility, or something correlated with sterility, is the chief cause of the slow development. This view was strengthened by the F_4-analysis. In this generation there was opportunity for comparing progenies of fertile as well as of partially sterile mother plants, both types segregating in red : T—C. Four countings were made.

1. STERILE PROGENIES.

As in F_3 the percentage of redflowered plants (table 9) shows a continuous increase from $4{,}3 \pm 1{,}8$ % to $31{,}5 \pm 2{,}9$ %. The difference $31{,}5 - 4{,}3 = 27{,}2 \pm 3{,}4$ is evidently significant.

2. FERTILE PROGENIES.

At the first counting there was $60{,}5 \pm 5{,}6$ % redflowered plants, at the last counting $71{,}5 \pm 3{,}6$ %. The difference, $11{,}0 \pm 6{,}7$, is not significant ($D/m_D = 1{,}6$), and consequently the segregation ratio has not been subject to any sure alteration.

In F_4 no classification in fertile and sterile was made until all plants had begun to flower. However, in the fertile progenies redflowered and T—C-plants showed no sure difference in speed of development, in contrast to the progenies of semisterile mother plants, where the redflowered plants were later than the T—C-types. As in the latter progenies most redflowered plants are sterile, most T—C-plants fertile, it may be concluded, that sterility is either the cause of the slow development or in any case more correlated with the cause, than are the flower colour factors.

In another cross (T—B × T—G), previously described (MÜNTZING 1930, pp. 203—206), correlation between flower colour type and rate of somatic development was also observed. However, in this cross where all plants were fertile and segregation ratios normal, individuals with red factors started flowering earlier than the recessive plants. This was supposed to be caused by a pleiotropic action of the red factors. In view of the present results, not pleiotropism but linkage between flower colour factors and other factors, influencing the rate of development, seems to be a more plausible explanation (cf. SIRKS 1929).

Why, then, are the partially sterile plants later than the fertile ones? It has been shown that in the present cross the lethal factors manifest themselves during the haplophase and cause the death of certain classes of gones. Therefore it may seem curious that these factors should also influence the somatic development of the mother plant. However, it may be remembered that all partially sterile plants in question have the constitution $\frac{l}{l}+\frac{L_1}{l_1}$, all fertile plants $\frac{l}{l}+\frac{L_1}{L_1}$. On basis of the translocation hypothesis (discussed in previous publications [MÜNTZING 1929, p. 315; 1930, p. 234]) it is natural that gametes carrying $l+L_1$ or $L+l_1$ are vital and gametes of the constitution $l+l_1$ or $L+L_1$ lethal (in the pollen) or sublethal (in the ovules). According to the same hypothesis $l+l_1$-gametes are deficient in chromatine material, $L+L_1$-gametes, on the contrary, have one piece of chromosome duplicated or *vice versa*. Then, turning to the somatic formulæ, $\frac{l}{l}+\frac{L_1}{L_1}$ and $\frac{L}{L}+\frac{l_1}{l_1}$ are balanced types, $\frac{l}{l}+\frac{L_1}{l_1}$ represents a deficiency (or duplication). If that is true, it is rather natural, that the lack of balance should also have some effect on the diplophase. This effect may be the slower growth of the partially sterile types.

OBSERVATIONS ON EMBRYO FORMATION.

Except some measurements of the number of seeds per calyx (MÜNTZING 1929, p. 306, table 6) the female fertility in the *Galeopsis*-crosses has hitherto not been subject to investigation. The genetic results, however, show that sterility is less pronounced in the ovules than in the pollen. In crosses where half of the pollen is bad, more than 50 per cent of the ovules must be functional. This also proved to be the case judging from the percentage of developing embryos observed

in sections of young and growing fruits (about 1—10 days after fertilization). In most cases all the four part-fruits from one flower were cut at the same time, and therefore there is no or slight risk that empty ovules will be overlooked. The sections were cut about 20 μ thick and stained in gentian violet. The following different types were investigated: F_1 of the present cross, T—B × T—C, F_1 of the cross T—B × T—X (see MÜNTZING 1929), and for comparison the pure lines T—B and T—X. The ovules were found to contain either developing embryos, unfertilized but otherwise apparently normal embryosacs or, thirdly, undeveloped or quite obliterated embryosacs. The results are given in table 10.

TABLE 10. *Embryo development in pure lines and sterile F_1-generations.*

Pure lines and F_1-generations	Number of ovules	Number of obliterated embryosacs	Number of unfertilized embryosacs	Number of developing embryos	Per cent of embryos
T—B, 1930	23	1	—	22	96
» , 1931	25	1	1	23	92
T—B, total	48	2	1	45	94
T—X, 1931	38	4	4	30	79
T—B × T—X, F_1, 1930	35	5	6	24	69
» , » , 1931	74	13	19	42	57
T—B × T—X, F_1, total	109	18	25	68	62
T—B × T—C, F_1, 1931	71	6	23	42	59

In the line T—B 94 per cent of the ovules contained developing embryos, in the line T—X the corresponding figure was somewhat lower (79 per cent). On an average the parent lines had embryos in 87 per cent of the ovules.

The partially pollensterile F_1-generations have a lower proportion of developing embryos. Seventyone ovules from a T—B × T—C F_1-plant showed 42 embryos, 23 apparently normal but unfertilized embryosacs and 6 obliterated sacs. The corresponding values of 109 ovules from T—B × T—X, F_1, were 68, 25 and 62. In this case 62 per cent of the young seeds contained embryos. On an average the parent lines T—B and T—X had 87 per cent of embryo development. This value

corresponds to full fertility. Then the value 62 per cent of embryos corresponds to 71 per cent of full fertility. The F_1-plant T—B × T—C has about the same value. Consequently, more than half of the embryosacs are functional, which is in agreement with the genetical results.

The non-functioning embryosacs are in most cases morphologically well developed and normal in appearance. However, if selective fertilization does not take place they must be physiologically bad, as in all probability there are sufficient quantities of functional pollen avialable.

As a possible explanation of the relative excess of fertile and deficit of sterile plants repeatedly observed, it was suggested that zygotic competition might be the cause. This competition might take place at different stages. The present observations on the developing embryos do not indicate selective competition during this stage. Only in rare cases the embryos gave the impression of being in a bad condition, and this was no more frequent in sterile plants than in fertile ones. Neither does selective germination of the seeds take place. Each F_3- and F_4-family was raised from a given number of seeds. The percentage of plants obtained was calculated for each family. No correlation was found between low percentage of plants and high percentage of sterile individuals in the progenies.

CYTOLOGICAL OBSERVATIONS.

In several genera (*Pisum*, *Datura*, *Zea*) intraspecific sterility has been found to be correlated with cytological complications, viz. the formation of rings or chains at the reduction division. Preliminary investigations in *Galeopsis* (MÜNTZING 1929, pp. 316—17) indicated that such irregularities do not occur in this genus. This view has been confirmed by additional observations.

Several F_3-plants belonging to different categories were investigated. (The buds were fixed in CARNOY for some minutes and then brought into KARPECHENKO's fluid. Sections were cut about 14 μ thick and stained in gentian violet.) Good heterotypic metaphases showed without exception regular pairing and no indications whatever of secondary association. Figs. 1—2 show the 16 bivalents in side view from one red fertile and one red semisterile F_3-plant. Regular pairing at the heterotypic metaphase was observed with certainty in two red semisterile plants, one red fertile, one redflowered plant, having about 75 per cent good pollen, and one T—C-plant with the same degree of fertility.

Also plants from the fertile F_1-generation T—B × T—L showed the same regular divisions. If multiple associations occur during prophase, they would, most probably, persist at least to the heterotypic metaphase. Therefore, it seems safe to conclude that chromosomal irregularities do not occur in the intraspecific *Galeopsis*-crosses, neither in fertile nor in partially sterile plants.

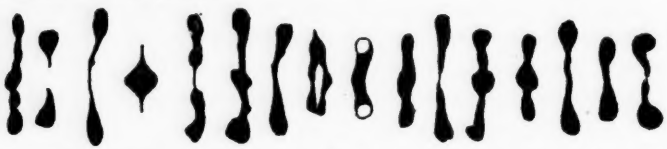

Fig. 1. Heterotypic metaphase from a fertile F_3-plant of the cross T—B × T—C. 16 bivalents, separately drawn.

Fig. 2. The same from a semisterile individual. × 3500.

DISTURBED SEGREGATION RATIOS IN THE CROSS T—C × »YELLOW TETRAHIT».

Similar disturbances as in the cross T—B × T—C, described above, were also observed in the cross T—C × »yellow *Tetrahit*». The latter line has in main the same type of white flower colour as T—B, only a little more yellowish. In F_1 the white colour was completely dominant over the T—C-type, in F_2 there was segregation in 94 white: 14 red : 16 T—C. The segregation of red F_2-plants shows that »yellow *Tetrahit*», just like the line T—B, is at the same time homozygous for one red-factor and one inhibitor. Then, the ratio 12 white : 3 red : 1 T—C should be expected. Evidently that ratio was not obtained, and it was therefore assumed that also in this cross selective elimination of recombination gametes might be responsible for the disturbed segregation.

The F_1-plants (8 individuals investigated) were partially pollen sterile, having an average of 61,9 per cent good pollen (MÜNTZING 1930, p. 229). In F_2 the pollen fertility showed the same bimodal variation (table 11) as in the other crosses of the semisterile type. Just as in the

cross T—B × T—C, however, the three different flower colour types were correlated with different distribution rates of pollen fertility. Most of the T—C-plants were fertile, most of the redflowered plants sterile, and among the dominant white plants some were sterile, others fertile. There can be no doubt that the categories red and T—C show a different variation in fertility. This makes the hypothesis probable that, also in this cross, the recombination gametes are completely eliminated in the pollen and partly eliminated in the ovules, the redflowered, sterile F_2-plants resulting from the union of one male recessive gamete and one female gamete, carrying the red factor and a pollen lethal constitution.

This view was confirmed by two F_3-progenies, one of which was raised from a fertile, the other from a semisterile redflowered F_2-plant (table 11, nos. 4—5).

The fertile F_2-plant (the pollen percentage being 95—100) gave in F_3 segregation in 42 red to 18 T—C-types which probably corresponds to normal monohybrid segregation. The progeny of the semisterile F_2-plant (which had an average of 56 per cent good

TABLE 11. *Pollen fertility in F_2 and F_3 of the cross T—C × »yellow Tetrahit».*

Table no.	Generation	Field number and type of flower colour	Good pollen 25—30	30—35	35—40	40—45	45—50	50—55	55—60	60—65	65—70	70—75	75—80	80—85	85—90	90—95	95—100 %	n	Flower colour of the mother plant	Pollen percentage of the mother plant
1	F_2	1930—54, white	—	—	1	3	3	4	7	3	2	2	2	4	6	16	40	93	white	60 (average)
2	»	» , T—C	—	—	—	—	—	—	—	—	1	—	1	1	1	4	8	16	»	»
3	»	» , red	—	—	1	1	1	1	3	—	—	—	2	—	1	2	2	14	»	»
1—3	»	total	—	—	2	4	4	5	10	3	3	2	5	5	8	22	50	123	»	»
4 a	F_3	1931—78, T—C	1	—	—	—	1	—	—	2	—	—	—	1	1	9	14	29	red	56
4 b	»	» , red	—	—	—	—	1	—	—	1	1	4	2	—	3	6	3	21	»	»
5 a	»	1931—79, T—C	—	—	—	—	—	—	—	—	—	—	—	—	—	3	4	7	»	98
5 b	»	» , red	—	—	—	—	—	—	—	—	—	—	—	—	—	3	15	18	»	»

pollen), on the contrary, segregated in 21 red : 29 T—C, giving the same excess of recessive plants as in the corresponding progenies of the cross T—B × T—C.

The pollen fertility was investigated in all descendants of the semisterile and in 25 descendants of the fertile mother plant. The latter plants were all fertile, the pollen percentage varying between 90 and 100. In the progeny of the semisterile mother plant the majority of the plants were fertile. However, about 43 per cent of the redflowered and 17 per cent of the T—C-plants were partially sterile (table 11). Thus, these progenies behave in all essentials as the analogous families of the cross T—B × T—C. Only the linkage between the red factor and one of the lethal factors seems to be weaker in the present cross.

The crossover value may be approximately determined by comparison between the number of fertile T—C and fertile red in the F_3-progeny of the semisterile mother plant (cf. above, p. 83). About 25 T—C and 12 red plants were obtained. If a and b are the frequencies of non-crossover and crossover gametes a : b will be = 1 : 0,22 and the percentage of crossover gametes will be about 18. In the cross T—B × T—C lower values were obtained.

The percentage of functioning female gametes, with pollenlethal constitution, may be roughly estimated by comparing the number of fertile and sterile F_3-plants (cf. p. 85). The ratio 37 : 13 was obtained, which gives the percentage 26. This value is about the same as in the previous cross.

DISCUSSION.

One of the presumptions of normal Mendelian segregation is equal viability of the different kinds of gametes produced by heterozygous individuals. The main result of the present investigation is the proof that, in the crosses analysed, different classes of gametes have different viability and that this differential viability is the cause of disturbed segregation ratios.

The progenies of heterozygous redflowered F_2- and F_3-plants are especially striking. If the mother plant is fertile, normal monohybrid segregation is obtained. If the mother plant is partially sterile, that means the death of all male and part of the female gametes, carrying the red factor. Consequently, the progeny will consist of a majority of recessive and a minority of dominant plants.

In the progeny of partially sterile species hybrids the segregation ratios are probably often complicated by selective sterility, even in

hybrids where no cytological complications occur. Such is e. g. probably the case in the cross *Galeopsis ochroleuca* × *angustifolia* (MÜNTZING 1930, pp. 307—309). In this cross 136 F_2-plants were obtained, of which 131 were dominant yellow-white like the *ochroleuca* parent and F_1, the remaining 5 being redflowered like *angustifolia*. This suggests a polymeric segregation in a cross between non-polyploid parents ($n = 8$). However, as F_1 is partially sterile, partial elimination of gametes, carrying the red factor, is a more plausible explanation.

Intraspecific sterility may not only cause deviations from expected segregation ratios. In certain cases the result may be an apparent linkage between different factors.

The F_2-segregation of the cross T—B × T—C, described in this paper, gave evidence of linkage between the factors *R* and *H* (see MÜNTZING 1930, p. 218), the gametic ratio being about 7 : 1. The analysis of the cross showed this linkage to be a pseudo-linkage caused by selective elimination of the recombination gametes.

In *Pisum* HAMMARLUND (1929) got evidence of a strong linkage between two pairs of factors, *A* and *Gp*. In certain crosses, however, the same factors gave free combination. On account of the similarity in experimental results between the cases in *Pisum* and *Galeopsis*, it was supposed (MÜNTZING 1930, p. 235) that something essentially similar caused the linkage in both genera. In fact, this proved to be the case. The *Pisum* plants, giving linkage in the progeny, proved to be semisterile in both pollen and ovules (HAMMARLUND and HÅKANSSON 1930) but, on the other hand, the plants giving free combination are fertile. Probably thus, the strong linkage observed by HAMMARLUND in *Pisum* represents another case of pseudo-linkage, caused by elimination of the recombination gametes. However, the possibility also remains that in *Pisum* sterility is not the direct cause of the linkage but only a parallel phenomenon. If, on basis of the translocation hypothesis (see HÅKANSSON 1931), one of the genes is situated in the translocated chromosome part, the K-line (giving linkage when crossed to the double recessive type) may have both genes in the same chromosome in contrast to the F-line (giving free combination), where the genes are situated in different chromosome pairs. However, as the chromosomal interchange has probably only affected a minor part of the chromosomes, it is at present more probable that the genes also in the K-line are situated in different pairs, and that the linkage observed is a false linkage, caused by selective sterility.

In his »Konversions-Theorie» WINKLER (1930) interprets HAMMAR-

LUND's results in terms of his linkage theory. However, the finding of sterility as a probable cause of pseudo-linkage in *Pisum* does not favour the application of WINKLER's theory to this case.

The cases of pseudo-linkage in *Pisum* and *Galeopsis* justify the following questions. How many of the observed cases of linkage are linkage *sensu stricto*, and how many are cases of pseudo-linkage? And which are those criteria, by means of which true linkage may be distinguished from pseudo-linkage? The cases of false linkage are caused by haplontic sterility. Consequently, the occurrence of partial sterility in crosses, where linkage is observed, gives reason to suspect that the linkage is only apparent and due to differential viability of the gones. Therefore, *when studying linkages and linkage values it is absolutely necessary to investigate the viability of the haplophase, if one wants to decide, whether the linkage is real or only apparent.*

In *Pisum* and *Galeopsis* it is easy to establish the occurrence of partial pollen sterility, in other cases this is more difficult. In some cases, for instance, the pollen may be morphologically perfect but nevertheless comprise different classes of gametes with different viability. Such is evidently the case in *Matthiola.* WADDINGTON (1929) has shown that in double-throwing singles, the pollen has a lower germination power than in no-double-throwing singles. In combination with other experimental facts, these results suggest that there is a factor in the double race, which is lethal to all pollen containing it. This would explain the non-functioning of pollen carrying singleness. PHILP and HUSKINS (1931) have made a cytological analysis of the *Matthiola* problems and among other things they have arrived at the following conclusions. The difference singleness—doubleness involves one chromosome pair, having trabants. In double-throwing singles, one of the chromosomes lacks the trabant. Gametes containing this deficient chromosome are lethal in the pollen, partially lethal in the ovules. There are also indications of embryosac competition (»Renner-effect»), which may lead to complete female fertility though in reality certain classes of gametes are eliminated. This is very interesting with regard to the cases of pseudo-linkage. Not only may the pollen be apparently normal, but also seed production quite good, and nevertheless selective elimination take place both in pollen and ovules. This leads to the extreme conclusion that *observed cases of apparent linkage have not been shown to be true linkages until embryosac development and pollen germination have been controlled.*

Besides the cases already mentioned in *Galeopsis*, *Pisum* and

Matthiola, intraspecific sterility has been shown to affect the segregation ratios in maize. BRINK (1929) states that certain linkage groups were affected by semisterility, and according to BURNHAM (1930) abnormal »shrunken» and »waxy» ratios furnish evidence that the *sh—wx* chromosome is one of those involved in »semisterile 2».

Though intraspecific sterility and self-sterility are quite different phenomena, it may be mentioned in this connection that self-sterility may also be the cause of disturbed segregation ratios. In *Nicotiana* BRIEGER and MANGELSDORF (1926, 1927) found deviating segregation results which were shown to be caused by linkage between flower colour factors and self-sterility factors. Finally, the many cases of disturbed segregation ratios, caused by pollen tube competition, may be remembered of (see JONES 1928). In fact, intraspecific sterility, pollen tube competition, and self-sterility represent different expressions of the viability of the haplophase and the interaction between haplo- and diplophase. Each of these phenomena upsets one of the presumptions of normal Mendelian segregation, viz. equal quantities and equal viability of the different types of gametes at the time of fertilization. Therefore, in all three cases the result may be disturbed segregation ratios.

As already mentioned, cases of intraspecific sterility are often correlated with cytological complications, viz. formation of multivalent rings or chains at the reduction division. These irregularities present strong evidence in favour of the hypothesis that translocation or segmental interchange are the ultimate causes of intraspecific sterility, at least in those cases where the cytological complications occur. In maize, for example, it has been definitely shown (MCCLINTOCK 1930, COOPER and BRINK 1931) that certain cases of semisterility are associated with reciprocal translocations between chromosomes which may be morphologically identified.

However, the correlation between sterility and the formation of multiple chromosome associations is not absolute (cf. MÜNTZING 1930, pp. 234—235; HÅKANSSON 1931, pp. 42—51). Especially interesting are such cases where fertility is correlated with special chromosome configurations (*Datura*, BLAKESLEE 1929). Probably, in these cases random chromosome distribution does not take place, the formation of lethal gamete combinations being prevented by a special type of chromosome arrangement and chromosome distribution.

To a certain degree such cases seem to elucidate the origin of chromosome chains in *Oenothera*, where in some forms regular zig-zag

arrangement leads to the formation of only two kinds of gametes, both of which are vital.

In *Galeopsis*, fertile as well as sterile types show regular pairing and no ring formation. This does not prove that translocations or segmental interchange have not taken place. Ring formation may be prevented e. g. by small size of the chromosome fragments exchanged or by low frequency of chiasma formation.

Originally another explanation of the cases of intraspecific sterility in *Galeopsis* was given (MÜNTZING 1929, pp. 313—314; 1930, pp. 276—277) and this hypothesis is still open. — On account of spontaneous species crosses between *G. Tetrahit* and *bifida*, each *Tetrahit*- and *bifida*-line may contain single chromosomes or genes derived from the other species. This may lead to the formation of lethal recombination gametes in crosses within the species.

In other cases such as in *Zea* and *Pisum*, intraspecific sterility is evidently not caused by species hybridization, but results from spontaneous or induced exchanges between non-homologous chromosomes. An intermediate situation seems to prevail in certain *Viola* crosses. According to CLAUSEN (1931) the F_1-plants of the cross *V. tricolor* × *Orphanidis* do not show much multivalent association but in later generations this phenomenon is more frequent. Therefore, as suggested by CLAUSEN, the conditions in hybrids may favour segmental interchange between non-homologous chromosomes. If such is the case also in other genera, the intraspecific sterility in *Galeopsis* may be caused both by species hybridization and segmental interchange.

SUMMARY.

1. Correlation between segregation of flower colour and partial sterility was found in a cross between pure lines of *Galeopsis Tetrahit*. The present paper gives the F_3- and F_4-results and additional data from another cross.

2. Fertile, heterozygous, redflowered plants give monohybrid segregation. Partially sterile plants of the same category give a majority of recessive, a minority of dominant descendants. This is due to elimination of all male and part of the female gametes carrying the red factor.

3. In all main respects fertility variation in different types of progenies is in accordance with expectation. Sterility is caused by lethal factors, linked to the flower colour factors.

4. The amount of crossover between the red factor and the lethal factor, linked to it, was estimated 5—10 per cent.

5. Gene combinations, which are lethal in the pollen, function to some degree in the ovules. In partially sterile red F_2-plants, about 70 per cent of the female gametes are »vital», about 30 per cent »sublethal».

6. In F_3 and F_4 correlation was found between flower colour type and speed of somatic development. The redflowered plants were slower than the recessive T—C-plants. This is probably not due to the flower colour factors as such, but to the fact that the redflowered plants are generally sterile, the recessive plants fertile. On basis of the translocation hypothesis the sterile plants in question represent cases of deficiency or duplication. This may influence the diplophase as well as the haplophase, and result in slower growth of the partially sterile plants.

7. Observations on embryo formation in fertile and partially sterile plants showed that in the sterile plants embryos are developed in more than half of the embryosacs, which is in agreement with the genetical results.

8. Cytological investigations showed that chromosome pairing is quite regular in fertile as well as in sterile plants. Multivalent formation does not occur.

9. Another cross within *G. Tetrahit* was analysed to F_3 and showed the same type of correlation between segregation of flower colour and sterility.

10. Differential gametic viability may lead, not only to disturbed segregation ratios, but also to pseudo-linkage. When studying linkages and linkage values, it is absolutely necessary to investigate the viability of the haplophase in order to decide, whether the linkage is real or only apparent. In extreme cases studies of embryosac development and pollen germination are the only means to settle the question.

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CYTO-GENETIC INVESTIGATIONS ON SYNTHETIC GALEOPSIS TETRAHIT

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INTRODUCTION.

THE general occurrence of polyploidy among the higher plants has, especially during the last decade, led to investigations of the causes and origin of multiple chromosome numbers. These rather central problems have been attacked in several ways, among which the experimental production of polyploids is of chief interest. By various methods it has been possible, either to cause the doubling of the same, or the summation of different genomes. The polyploid types thus obtained are — especially in cases of allo-polyploidy — in many respects comparable to new species. Hence it has been concluded that polyploid species found in nature have originated in similar ways.

In later years an ever increasing number of cases of allo-polyploidy have been described and discussed. Also in the genus *Galeopsis*, investigated by the present writer, the formation of allo-polyploids has been studied (MÜNTZING 1930 a and b). To give a short recapitulation this case was as follows. Crosses between the species *G. pubescens* and *speciosa*, both having the haploid chromosome number 8, gave highly sterile F_1-hybrids. However, an F_2-generation was raised, comprising about 200 individuals. One F_2-plant was found to be triploid and almost completely sterile. After pollination with pollen from one of the parents, *pubescens*, the triploid plant produced one single seed. This seed gave a tetraploid plant with good fertility.

This case of chromosome increase after species crossing is especially interesting as it elucidates the origin of the »natural» tetraploid species *G. Tetrahit* L. As previously described in detail (1930 a, pp. 291—93; 1930 b, pp. 154—158) both the triploid F_2-plant and its tetraploid daughter were morphologically undistinguishable from pure *Tetrahit*. Further, the artificial tetraploid behaved like a true *Tetrahit* not only morphologically but also in genetical and — as far as could be observed — also in cytological respects (see 1930 b, p. 158). Therefore, the triploid F_2-plant was called »pseudo-*Tetrahit*» and its tetraploid descen-

dant »AT». (artificial *Tetrahit*). On account of these and other facts (see 1930 a, p. 294) the conclusion was drawn that not only the artificial tetraploid but probably also natural *G. Tetrahit* represents a synthesis of *pubescens-* and *speciosa*-genomes. Consequently, this case might be regarded as the first instance where a species already existing in nature has been synthesised from the genomes of two other species.

The primary tetraploid, the AT-plant, was used both for selfing and for crosses with natural *Tetrahit-* and *bifida*-lines. The progeny obtained from selfing of the AT-plant may be called the I_1-generation of artificial *Tetrahit*, or better, in order to emphasize the mode of origin, the I_1-generation of *synthetic Tetrahit*.

THE I_1-GENERATION.

Methods. — From the AT-plant seeds were harvested, partly from free flowering, partly from controlled selfing (double bags). Though the plant was grown in a pot a good distance apart from the other *Galeopsis*-cultures only seeds from the bags were used for raising the I_1-generation in spring 1931.

On account of the similarity of synthetic and natural *Tetrahit*-plants special precautions had to be undertaken in order to avoid intermixtures. The seeds were as usual (cf. 1930 a, p. 190) brought to germination in bags of moist blotting paper. The seedlings were then pricked out in boxes with sterilised soil. After about ten days the young plants were planted separately in small pots in order to get root tips for cytological purposes. When planted in the pots the plants were all marked with a piece of wool, which remained when later on the plants had been transplanted into the field. Here each plant was labelled separately, and the growing generation was watched daily. Therefore, all plants belonging to the I_1-generation were with absolute certainty descendants from selffertilization of the AT-plant.

The I_1-generation was raised from 276 seeds. These gave 190 seedlings of normal appearance. By overheating in a hot-bed about 60 seedlings were killed, by another accident 29 young plants were lost. Most of the remaining 101 plants were grown in the experimental garden. Here 7 plants died from attacks of some fungus disease which this year ravaged in the *Galeopsis*-cultures. The remaining 94 plants reached maturity and were investigated with the following results.

I. MORPHOLOGY OF THE I_1-GENERATION.

1. HEIGHT AND HABITUS.

The height of the plants varied from 30 to 140 cm. (table 1). Two plants were clearly aberrant in habitus. In comparison with the other plants they were dwarfs, the height being 30—40 cm. One of them was well-proportioned, the other had peculiar leaves with big coarse leaf-dents. Most of the plants, however, were quite normal in appearance and on an average rather vigorous. One plant reached a height of 137 cm. and the average value of I_1 was $95{,}90 \pm 2{,}04$ cm. The average height of the original parent strains of *pubescens* and *speciosa* was this year $84{,}65 \pm 1{,}11$ and $78{,}75 \pm 2{,}62$ cm. The differences between I_1 and *speciosa* and *pubescens* are $11{,}25 \pm 2{,}34$ ($D/m_D = 4{,}81$) and $17{,}15 \pm 2{,}47$ ($D/m_D = 6{,}94$) resp. Thus, the tetraploid synthetic forms seem to be more vigorous than the diploid parents. Also the triploid pseudo-*Tetrahit*-plant and the primary tetraploid, AT, were well developed and reached a height of 98 and 114 cm. resp.

However, as in some details the treatment of the seedlings may have favoured the development of the I_1-generation more than that of the parent strains, I_2 results will be awaited before quite sure conclusions can be drawn concerning the vigour of the synthetic types.

Besides height variation differences in the general appearance of the plants were caused by variable types of ramification. One plant had strikingly long main branches and few lateral ones. But such deviations from the ordinary type may be found also within *G. Tetrahit* L., and except the two aberrant dwarf plants the I_1-individuals were really in habitus very like different types of natural *Tetrahit*.

2. FLOWER TYPE AND FLOWER SIZE.

All the 94 I_1-plants were redflowered like the mother plant, AT, and the grandmother plant, pseudo-*Tetrahit*. However, variation in the nuance of red was obvious, 10 plants being light red or light yellowish red, the other plants being more dark and pure red. It may be remembered that of the original parents, the *pubescens*-biotype used for the cross is redflowered, the *speciosa*-biotype, as always, yellow. The triploid pseudo-*Tetrahit* was light yellowish-red, the mother plant, AT, was more purely red but still with a tinge of yellow.

Concerning the *type of network*, which is an important species character in the subgenus *Tetrahit* (cf. 1930 a, p. 237) the I_1-plants could be classified in four, not sharply separated categories: 1) The net

TABLE 1. *Height variation.*

	Height in cm. 30–35–40–45–50–55–60–65–70–75–80–85–90–95–100–105–110–115–120–125–130–135–140																						n	M ± m
pubescens	—	—	—	—	—	—	—	1	3	10	10	10	8	3	1	—	—	—	—	—	—	—	46	84,65 ± 1,14
speciosa	—	—	—	—	—	1	3	—	2	5	3	4	—	1	1	—	—	—	—	—	—	—	20	78,75 ± 2,62
Synthetic *Tetrahit*, I_1...	1	1	—	—	—	1	4	6	5	4	7	7	13	13	4	7	7	3	3	—	1		87	95,90 ± 2,04
AT × *Tetrahit*	—	—	—	—	—	1	—	—	—	1	2	4	5	5	8	10	4	2	2	2	—		46	106,75 ± 1,98
» × *bifida*.....	—	—	—	—	—	—	—	—	—	—	—	1	2	—	2	2	—	—	1	—	1		9	110,30
Six *Tetrahit*-lines, total	—	—	—	—	—	1	2	11	12	20	14	11	10	1	9	8	8	4	—	—	—	—	111	86,80 ± 1,45
Four *bifida*- » »	—	—	1	—	1	7	5	3	9	10	12	9	7	7	1	1	—	—	—	—	—	—	73	78,85 ± 1,59

TABLE 2. *Flower length.*

	Flower length in mm. 13–14–15–16–17–18–19–20–21–22–23–24–25–26–27–28–29–30–31																			n	M ± m
speciosa, 1931—151	—	—	—	—	—	—	—	—	—	—	—	—	3	2	8	9	5	—	—	27	27,41 ± 0,24
pubescens, » —154	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	7	13	10	33	29,88 ± 0,18
Tetrahit (9 pure lines)	—	—	—	3	12	33	47	40	23	11	1	—	—	—	—	—	—	—	—	170	19,34 ± 0,12
bifida (5 pure lines) ...	1	16	44	23	13	6	—	—	—	—	—	—	—	—	—	—	—	—	—	103	15,48 ± 0,11
Synthetic *Tetrahit*, I_1...	—	—	3	8	7	13	21	18	12	3	7	1	—	—	—	—	—	—	—	93	19,23 ± 0,21
Tetrahit × AT (total)...	—	—	—	—	7	14	12	11	9	6	—	1	—	—	—	—	—	—	—	60	20,60 ± 0,21
bifida × » » ...	—	—	—	—	4	4	5	5	2	—	—	—	—	—	—	—	—	—	—	20	18,85 ± 0,29

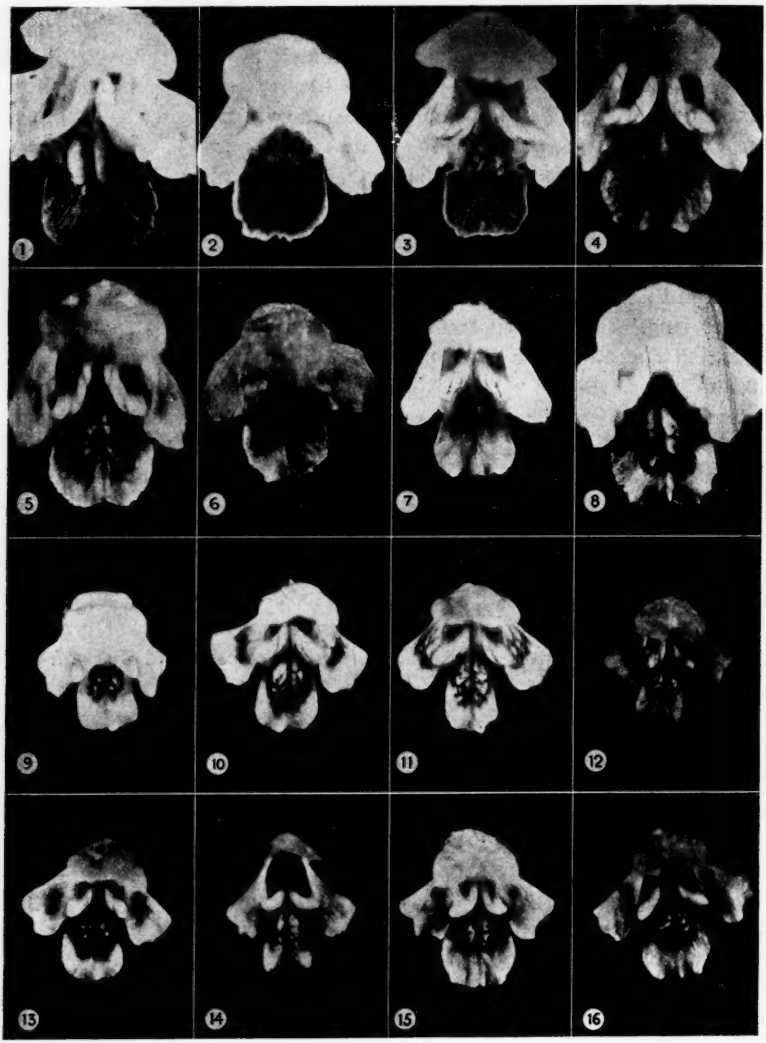
of the same type as in »typical» *Tetrahit*-lines. 2) The net as in the mother plant, AT, not quite distinct, though nevertheless of *Tetrahit*-type. 3) Net more or less diffuse or running towards the edge of the lap. 4) Clearly aberrant types, where the network is different from that found in pure *Tetrahit*-lines. The number of plants belonging to the categories 1—4 were 19, 44, 12 and 19 resp. That is to say, in respect of the network 44 plants were of the mother type, 19 individuals were if possible still more typical *Tetrahit*, 12 were slightly aberrant, and 19 had network of a type not found in natural *Tetrahit*-lines.

As to *flower size* the following results were obtained (table 2). (Each individual value is the average of three flowers measured). The flower length in I_1 varied from 15 to 24 mm. and was on an average $19{,}23 \pm 0{,}21$ mm. The mother plant, AT, had a mean flower length of $19{,}86$ mm. (see 1930 b, p. 154). Thus, though there was a considerable variation, the descendants had on an average the same flower length (and flower size) as the mother plant. They had also the same flower length as natural *Tetrahit*. For comparison flowers from 170 individuals, belonging to 9 different pure lines of this species, were measured. This gave the average value $19{,}34 \pm 0{,}12$ mm. The original parents, *pubescens* and *speciosa*, were big-flowered as always, the average values being $29{,}38 \pm 0{,}18$ and $27{,}41 \pm 0{,}21$ resp. (cf. also 1930 a, table 31, p. 282).

Figs. 1—48 illustrate better than descriptions the flower type and flower size in the natural species *speciosa*, *pubescens* and *Tetrahit* and in the I_1-generation of synthetic *Tetrahit*.

Figs. 1—3 represent three *speciosa*-biotypes (from Roumania, Poland and Sweden resp.). They are rather big-flowered, the middle lap of the lower lip is diffusely violet and the network, when visible, almost or quite reaching the margin of the lap. Figs. 5—8 represent four different *pubescens*-biotypes. Figs. 5 and 6 are redflowered, 7 and 8 white-yellow. Fig. 8 shows the network to be of the *Tetrahit*-type. The biotype represented by fig. 5 has also a network of similar type, not reaching the margin of the lap. This biotype is the one used for the production of the synthetic *Tetrahit*-forms. It was crossed with the Swedish *speciosa*-biotype seen in fig. 3. The diploid F_1-generation is represented by fig. 4.

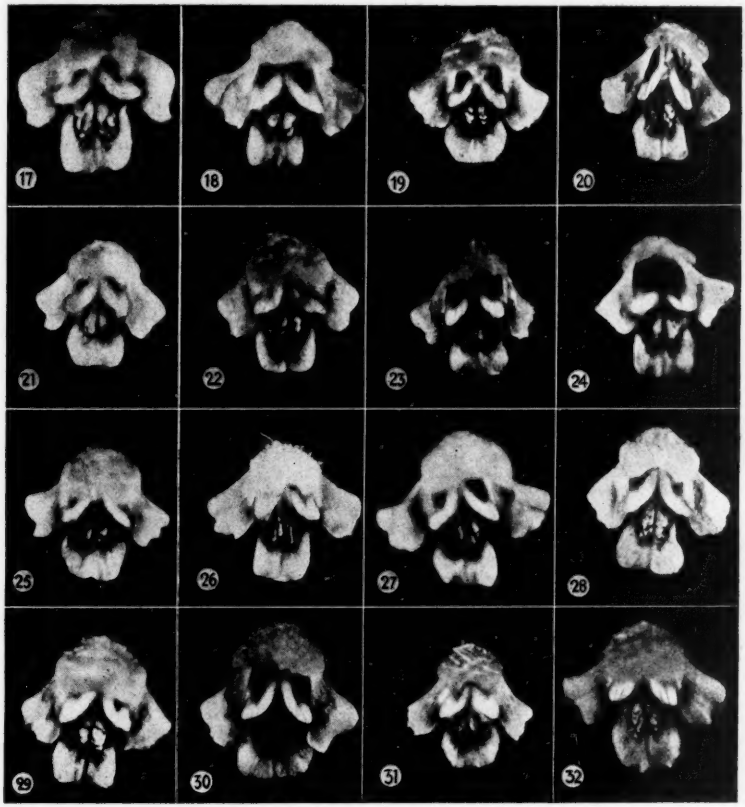
The flower type of natural *Tetrahit* is shown by figs. 9—16 (eight different pure lines). Those lines are all relatively small-flowered and if the network is marked (which is not always the case; cf. fig. 14) it never reaches the margin but is more or less restricted to an area at the basis of the lap. Otherwise in this species there is considerable



Figs. 1—3. *G. speciosa.* Three biotypes from Roumania, Poland and Sweden resp.; fig. 4. *G. pubescens* × *speciosa*, F_1. (The parents are represented by figs. 3 and 5.) — Figs. 5—8. Four different biotypes of *G. pubescens*; figs. 9—16, eight different biotypes of *G. Tetrahit* (T—B, T—D, T—E, T—F, T—G, T—I, T—L and T—M resp.). — Magnification: 2,5 ×.

variation in flower colour as well as in other details of the flower (cf. 1930 a, pp. 192—202).

Figs. 17—32 show flowers from I_1-plants of synthetic *Tetrahit*, which belong to the categories 1 and 2 (cf. above p. 107). The close

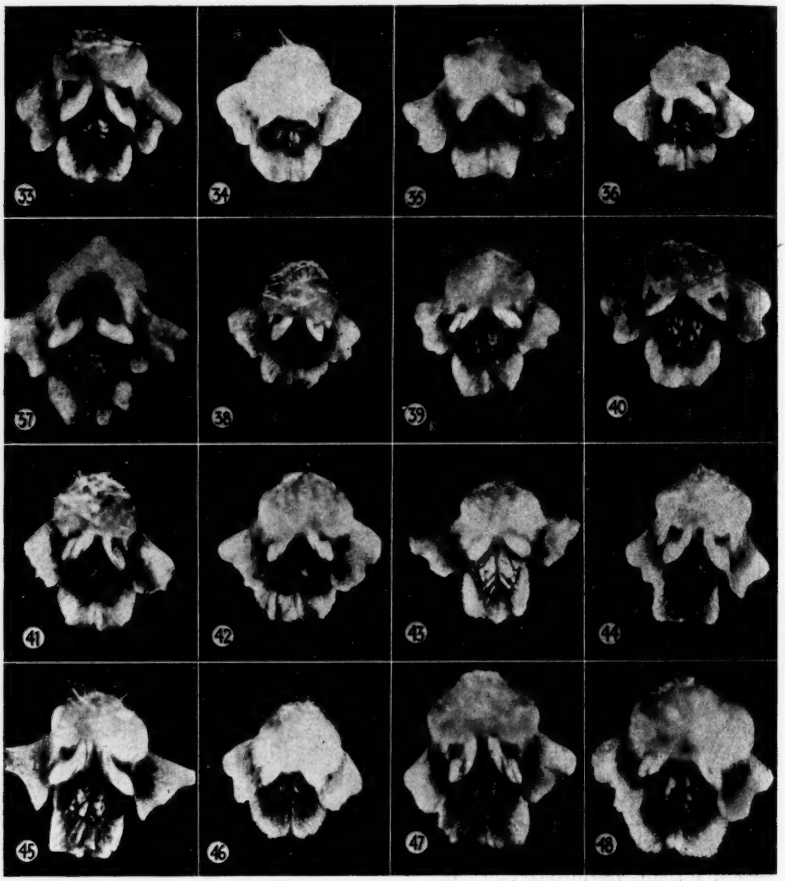


Figs. 17—32. Synthetic *G. Tetrahit*. Flowers from 16 different I_1-individuals. Note the similarity to figs. 9—16 (natural *Tetrahit*). — Magnification: 2,5 ×.

resemblance to the natural *Tetrahit*-flowers in figs. 9—16 is evident and striking, especially in comparison with the original parent biotypes of *pubescens* and *speciosa* (figs. 5 and 3). *There is no morphological criterium by means of which the flowers of these I_1-plants may be distinguished from those of natural Tetrahit.*

Figs. 33—48 represent flowers from another collection of I_1-plants.

Most of these belong to categories 3 and 4, that is, they are more or less deviating from typical *Tetrahit* and some of them are clearly aberrant (*e. g.* figs. 44—48).

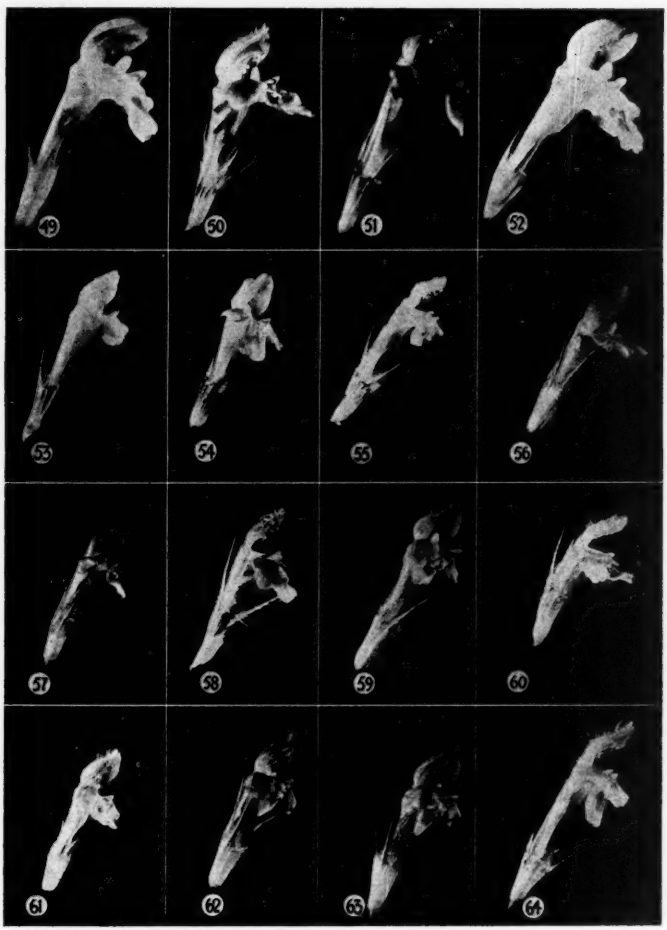


Figs. 33—48. Synthetic *G. Tetrahit* (continued). Flowers from 16 other I_1-plants, which are less typical or aberrant. — Magnification: 2,5 ×.

3. CALYX LENGTH.

The calyx length at time of flowering was measured in I_1 and in the parental biotypes of *pubescens* and *speciosa* (table 3). *G. speciosa* has a big calyx in contrast to *pubescens,* the average values being

$18{,}_{90} \pm 0{,}_{26}$ and $12{,}_{09} \pm 0{,}_{13}$ resp. Like the diploid F_1, *pubescens* × *speciosa*, the synthetic *Tetrahit*-types are intermediate ($M = 15{,}_{79} \pm 0{,}_{16}$). Though at present no data are available, it may be stated that on an



Figs. 49—64. Corolla and calyx in side view. Fig. 49. *G. speciosa*, fig. 50, *pubescens* × *speciosa*, F_1; fig. 51, *pubescens*; fig. 52, another *pubescens*-biotype. — Figs. 49—51 correspond to figs. 3—5, fig. 52 to fig. 8. — Figs. 53—56, four biotypes of natural *Tetrahit* (T—B, T—D, T—L and T—M); figs. 57—64, synthetic *Tetrahit*, eight I_1-plants. Fig. 64 is an aberrant trisomic I_1-plant also represented by fig. 48. — Magnification: 1,5 ×.

TABLE 3. *Calyx length.*

	Calyx length in mm. 11	12	13	14	15	16	17	18	19	20	n	M ± m
speciosa, 1931—151	—	—	—	—	—	—	4	3	5	9	21	$18{,}90 \pm 0{,}26$
pubescens, » —154	3	14	5	—	—	—	—	—	—	—	22	$12{,}09 \pm 0{,}13$
pubescens × *speciosa*, F_1	—	—	3	4	—	—	—	—	—	—	7	$13{,}57$
Synthetic *Tetrahit*, I_1 ...	—	2	2	11	31	16	15	13	1	1	92	$15{,}79 \pm 0{,}16$

average the calyx dimensions of natural *Tetrahit* are also intermediate between the extremes represented by *speciosa* and *pubescens*.

Figs. 49—64 give an idea about the calyx dimensions (cf. also 1930 b, fig. 6) and the relative length of calyx and corolla. Fig. 49 shows the big calyx and corolla of *speciosa*, fig. 51 represents the *pubescens*-biotype used for the crosses, fig. 52 is another *pubescens*-biotype, fig. 51 is *pubescens* × *speciosa*, F_1. In the *pubescens*-biotypes the corolla is generally more than twice as long as the calyx. In *G. Tetrahit* the calyx is relatively bigger, though a considerable variation occurs. Figs. 53—56 show four different *Tetrahit*-lines of which nos. 54 and 56 represent two different extremes in respect of calyx size. Finally, figs. 57—63 show seven individuals of the I_1-generation, chosen at random. It is evident that these I_1-plants also in respect of calyx dimensions and the relative length of calyx and corolla are of the same type as natural *Tetrahit* biotypes. Fig. 64 is an aberrant, rather *pubescens*-like I_1-plant (the same as in fig. 48). This plant proved to be trisomic, having 33 instead of 32 chromosomes (see below, p. 127).

4. LEAF SHAPE.

In the representatives of the subgenus *Tetrahit* leaf shape is very variable. There are, however, some characteristic differences between *pubescens* and *speciosa* (cf. 1930 b, p. 157). In *G. Tetrahit* the leaves are more or less intermediate, though in some lines (perhaps the majority) they are more like those of *speciosa*, in other lines more like those of *pubescens*. The pseudo-*Tetrahit* and AT-plants had leaves which might be regarded as being of *Tetrahit*-type. In the I_1-generation leaf shape was variable, sometimes remembering the *speciosa*-parent, sometimes *pubescens*. But on an average the leaves showed the intermediate conditions found in pure *Tetrahit*. Measurements were made but they are incomplete on account of *Aphis*-attacks which destroyed the normal leaf shape in many of the plants. Therefore, further data from I_2 and

Fig. 65.

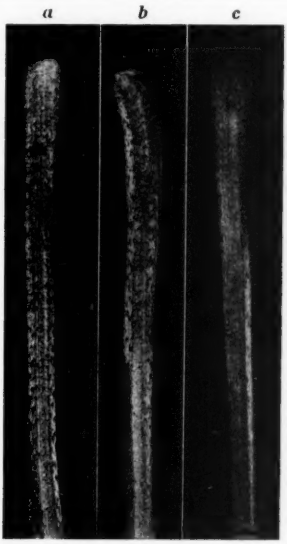


Fig. 66.

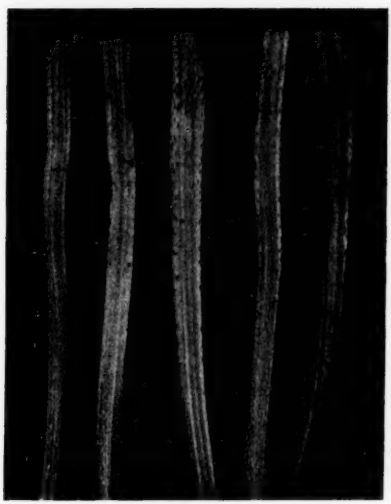


Fig. 67.

Figs. 65—67. Internodes of *G. speciosa* and *pubescens*. Fig. 65, four different *speciosa*-biotypes; fig. 66 *b*, *pubescens* × *speciosa*, F_1; fig. 66 *a* and *c*, the parental biotypes (*a*: *speciosa*, *c*: *pubescens*); fig. 67, five other *pubescens*-biotypes. — Natural size.

later generations must be collected before definite conclusions may be drawn.

Fig. 68.

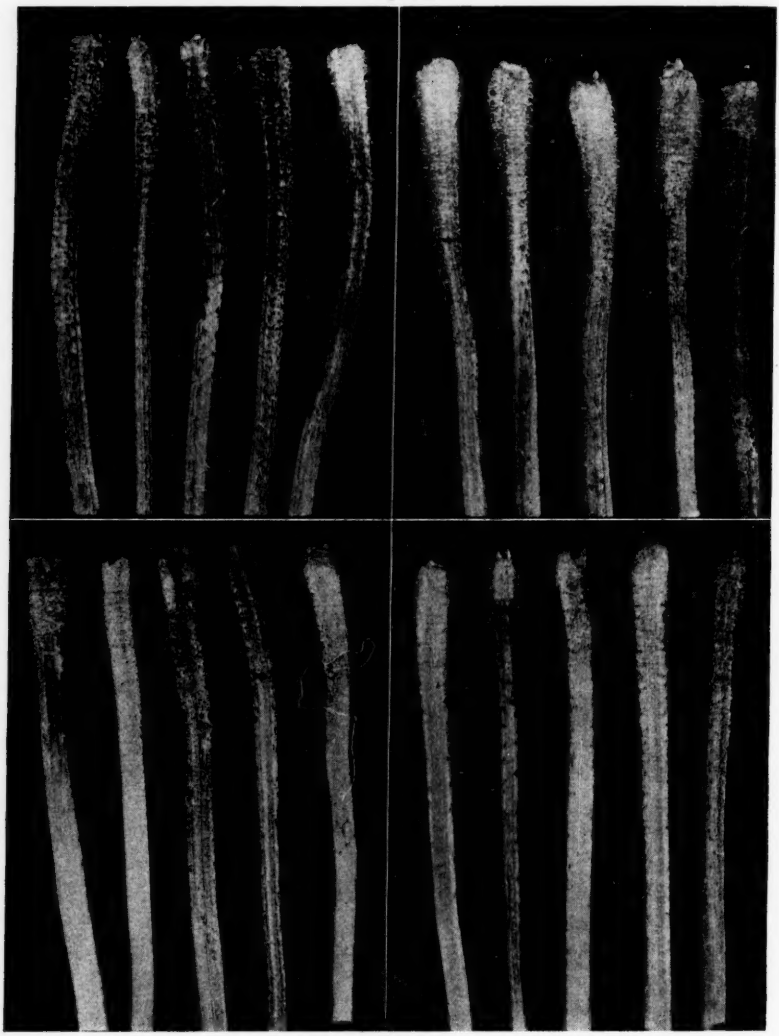


Fig. 69.

Fig. 68. Internodes of synthetic *Tetrahit* (ten different I_1-plants). — Fig. 69. Internodes of ten different pure lines of natural *Tetrahit*. — Natural size.

5. TYPE AND DEGREE OF HAIRINESS.

The type of hairiness of the four species *pubescens*, *speciosa*, *Tetrahit* and *bifida* has been described previously (1930 a, pp. 237, 282 and 295; 1930 b, p. 157). In short, *speciosa* is characterized by plenty of bristle hairs which in typical cases are absent in *pubescens*. That species

TABLE 4. *Degree of bristle hairiness.*

	0	0—1	1	1—2	2	2—3	3	Total
Synthetic *Tetrahit*, I_1	—	3	15	17	55	2	—	92 individuals
Tetrahit-biotypes	—	—	5	4	5	1	—	15 biotypes
bifida- »	—	—	—	—	5	4	—	9 »
speciosa- »	—	—	—	—	4	1	1	6 »
pubescens- »	1	3	1	—	1	2	—	8 »

has instead soft hairs in greater quantity than in *speciosa*. Figs. 65 and 66 *a* show internodes of five different *speciosa*-biotypes, figs. 66 *c* and 67 the same from six *pubescens*-biotypes. Fig. 66 *b* represents the primary diploid F_1-hybrid from the cross *pubescens* (66 *c*) × *speciosa* (66 *a*). Obviously F_1 is intermediate. In fig. 68 internodes from ten individuals of synthetic *Tetrahit*, I_1, show a mixture of soft and bristle hairs, which is in agreement with the mode of origin of these plants. For comparison fig. 69 shows internodes of ten different lines of natural *Tetrahit*. If there is any difference between figs. 68 and 69 this should be that the synthetic forms are more intensively hairy than natural *Tetrahit*, especially in regard to the soft hairs. It was also noted that in several of the I_1-plants flowers and calices were more hairy than is perhaps the rule in natural *Tetrahit*. However, this possible difference is by no means certain, since there was a considerable variation in degree of hairiness among the I_1-plants,

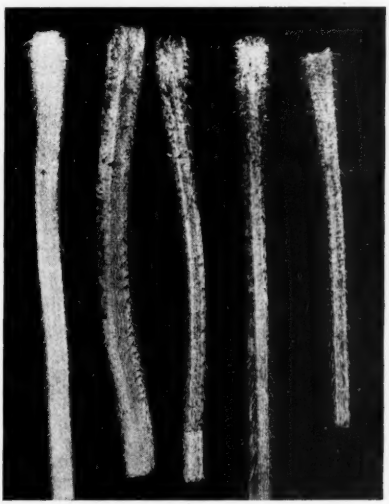


Fig. 70. Internodes of five different pure lines of *G. bifida*. — Natural size.

and as in this respect natural *Tetrahit*-lines are also rather different. The degree of bristle hairiness was estimated, using figure denominations from 0 (total absence) to 3 (see table 4). Besides the difference between *speciosa* and *pubescens* these estimations show or indicate that in respect of bristle hairiness *bifida* is more similar to *speciosa* than is *Tetrahit* (cf. fig. 70 which shows internodes from five *bifida*-lines). Further, both synthetic and natural *Tetrahit* are intermediate between *pubescens* and *speciosa*.

Summarizing the review of morhpological characters of the I_1-generation, we may say that these plants were vigorous and in habitus like natural *Tetrahit*-plants. They were also small-flowered and had calyx dimensions, leaf shape and type of hairiness as in this species. Concerning the network on the middle lap, two thirds of the plants fulfilled all claims of typical *Tetrahit*-pattern, one third, however, was more or less deviating.

In all morphological respects the I_1-generation was variable and certainly this variation was too great to be caused solely by environmental conditions. On the contrary, there must have been a considerable genotypical diversity among the plants.

II. FERTILITY OF THE I_1-GENERATION.

The pollen fertility of 97 I_1-plants was investigated (table 5, uppermost). The percentage of good pollen was determined in the usual way (cf. MÜNTZING 1929, pp. 297 and 299—300). However, in the present case the work was complicated by somatic disturbances. Ten plants were found to have deficient anthers and rather bad pollen. A few plants showed no external anther abnormalities but the pollen in these plants had a tendency to stick together in lumps. The great majority of plants, however, did not show any obvious disturbances of pollen development from the side of the mother plant.

In partially sterile plants the sterility may be either haplontic, that is, caused solely by lethal genotypical constitutions of the haplophase, the gones, or diplontic, caused by the mother plant (MÜNTZING 1930 a, pp. 314—322). Clear cases of haplontic sterility in *Galeopsis* have been analysed (MÜNTZING 1929, 1930 a, 1932) but also cases of diplontic sterility have been met with, *e. g.* in segregation products of the cross *Tetrahit* × *bifida*. In cases of purely haplontic sterility the anthers are quite normally developed, the difference between »good» and »bad» pollen is sharp, and the percentage of good pollen in a given plant is

TABLE 5. *Pollen fertility.*

	Per cent good pollen 5—10—15—20—25—30—35—40—45—50—55—60—65—70—75—80—85—90—95—100 %																			n	M
I_1, normal anthers ...	—	—	—	—	—	2	2	2	2	6	5	10	14	10	10	11	7	1	—	82	68,35 ± 1,53
», pollen lumped	—	—	—	—	—	1	—	—	—	3	1	—	—	—	—	—	—	—	—	5	49,50
», deficient anthers ...	1	1	1	1	1	1	2	1	—	—	1	—	—	—	—	—	—	—	—	10	29,50
T—A × AT and recipr.	—	—	—	—	—	—	—	—	—	—	—	—	1	1	5	3	—	4	—	14	81,80
T—B × »	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	—	—	—	3	77,50
T—C × »	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	52,50
T—D × » and recipr.	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	3	1	—	—	6	80,00
T—E × »	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	2	70,00
T—F × »	—	—	—	—	—	—	—	2	2	1	3	1	—	—	—	—	—	—	—	9	51,95
T—I × »	—	—	—	—	—	1	1	2	1	4	—	1	—	—	—	—	—	—	—	10	47,50
T—M × »	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	1	1	5	77,50
T—N × »	—	—	1	—	—	—	1	1	2	1	1	2	—	—	1	—	—	—	—	10	50,50
B—A × AT	—	—	—	—	—	1	—	1	1	—	2	—	—	—	—	—	—	—		5	47,50
B—B × »	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	35,00
B—E × » and recipr.	—	1	—	1	1	—	1	3	1	—	—	—	—	—	—	—	—	—	—	8	34,40
B—F × »	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—	3	44,15
bif. Roumania × AT	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	32,50
T—A × AT, F_2	1	—	—	—	—	—	2	2	2	4	2	2	2	6	4	4	1	2	—	34	64,55 ± 3,19
pubescens, 1931—154 ...	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	4	3	1	2	12	85,85
speciosa, » —151 ...	—	—	—	—	—	1	—	2	3	5	3	1	1	—	—	—	1	11	1	29	69,90

relatively constant. In cases where the pollen is bad, due, in part or exclusively, to unfavourable maternal influences, the anthers are often not normally developed, the pollen has a tendency to stick together in lumps, the difference between good and bad pollen is fluent and, finally, the percentage of good pollen is quite variable from time to time and in different flowers.

In the present case it is obvious that such somatic disturbances play a rôle and tend to decrease the percentage of good pollen. This may be the case also among some plants belonging to the majority of the I_1-plants, which do not show any *visible* signs of bad maternal influences. However, in this category the average pollen fertility was as high as $68{,}35 \pm 1{,}53$ % (table 5) and 39 plants out of 82 had from 70 to 95 per cent good pollen. The mother plant, AT, had the average pollen percentage 69 (1930 b, p. 158). Consequently, *almost half of the daughter plants show an increase of pollen fertility.* Especially interesting is the segregation, already in this generation, of a plant with 90—95 % good pollen, thus showing the same high degree of fertility as homozygous plants in pure lines of natural *Tetrahit.* This plant (200—32) also happened to belong to the »first category» in respect of flower colour pattern and is represented by fig. 24.

For comparison the percentage of good pollen was this year also investigated in the original parent strains of *pubescens* and *speciosa.* The result was in part surprising. The *pubescens*-biotype had an average of 85,85 % good pollen (table 5, lowest). The 29 *speciosa*-plants examined could be divided in two groups, one fertile, comprising 13 plants and the other group clearly sterile, comprising 16 plants. The slight sterility among the *pubescens*-plants is probably modificatory, as this pure line is morphologically quite constant and on several previous occasions has shown full fertility (cf. 1930 a, p. 281). Concerning *speciosa* the situation is different. This species, at least the strain used for the original cross *pubescens* × *speciosa*, is normally cross-fertilizing but is not selfsterile (cf. 1930 a, p. 189). On account of bad seed production in the isolation bags this strain has from time to time been propagated from seeds of openpollinated flowers and is therefore probably not quite homozygous. This may in part explain the sterility observed. By repeated observations on the degree of pollen fertility it was controlled that genotypical causes and not environment were responsible for the production of bad pollen. Moreover, bad pollen in the same strain was observed already in 1929 in a minority of the plants examined (cf. 1930 a, p. 281).

On an average seed production was found to be good in the I_1-generation. Some plants yielded abundant quantities of seed, others less. Plants with deficient anthers were observed to give few seeds in the bags but plenty of seeds on openpollinated branches. Consequently, there is reason to assume that also in the present case sterility was less pronounced on the female side than on the male.

HYBRIDS BETWEEN SYNTHETIC TETRAHIT AND NATURAL TETRAHIT AND BIFIDA.

I. MORPHOLOGY OF THE F_1-HYBRIDS.

As previously reported (1930 b) the primary synthetic tetraploid, the AT-plant, could be crossed without difficulty with natural *Tetrahit* and *bifida*, which are also tetraploid, but not with the diploid parents, *pubescens* and *speciosa*.

Crosses with *Tetrahit* gave in all 95 seeds (1930 b, table 1) from which 61 hybrids were obtained. For crosses with *bifida* the corresponding figures were 55 and 20. To these plants, which by morphological qualities and fertility conditions proved to be true hybrids, may be added one *Tetrahit*- and six *bifida*-plants which were of purely maternal type, and therefore most probably the result of unintentional selfpollination. Some plants died from various external influences, but no plants gave the impression of being genotypically weak or unviable. On the contrary, the hybrids obtained were on an average very vigorous (table 1). The average height of the hybrids with *Tetrahit* was $106{,}75 \pm 1{,}98$ cm. The average height of six *Tetrahit*-lines (used for the crosses) was $86{,}80 \pm 1{,}15$, and of four *bifida*-lines $78{,}85 \pm 1{,}59$ cm. The vigour of the hybrids with *bifida* was especially striking in such progenies where true hybrids were growing side by side with maternal plants from unsuccessful pollinations.

The *flower length* was also measured (table 2). The hybrids between *Tetrahit* and AT had the average $20{,}60 \pm 0{,}21$ mm. which is a little more than the corresponding values of synthetic *Tetrahit*, I_1, ($19{,}23 \pm 0{,}21$) and of natural *Tetrahit* ($19{,}34 \pm 0{,}12$). The hybrids between AT and *bifida* had the average flower length $18{,}85 \pm 0{,}29$ mm. and pure *bifida* $15{,}43 \pm 0{,}11$ mm. This seems to show that the hybrid vigour is noticeable also in respect of flower length.

Concerning the type of network and habitus of the flower, the F_1-hybrids with *Tetrahit* had in practically all cases typical *Tetrahit*-flowers, those with *bifida* were of the same type as in hybrids between

natural *Tetrahit* and *bifida*. However, slight variation was observed, obviously due to the fact that different kinds of gametes were produced by the AT-plant. But this variation was not so great as in the I_1-generation, and clearly aberrant flower colour types were not produced.

In the F_1-hybrids between AT and the *Tetrahit*-lines T—A and T—B the flower colour was dominant white, due to the presence of the inhibiting factor *H*, carried by those *Tetrahit*-lines (cf. 1930 a, p. 202). It is interesting to see that this factor is epistatic to the red factors of synthetic *Tetrahit* (derived from *pubescens*) just as to the red factors of natural *Tetrahit*. — In all other F_1-generations the flower colour was red, as the *Tetrahit*- and *bifida*-lines used were either redflowered or recessive to the redfactors from AT.

In regard of leaf shape, hairiness and other vegetative characters the hybrids with *Tetrahit* were undistinguishable from pure *Tetrahit*, the hybrids with *bifida* were of the same type as hybrids between natural *Tetrahit* and *bifida*. The F_1-generations were not quite uniform, but compared with the I_1-generation the variability was evidently diminished, due to homozygosity of the pure lines of natural *Tetrahit* and *bifida*.

II. FERTILITY OF THE F_1-HYBRIDS.

1. FERTILITY IN CROSSES BETWEEN AT AND TETRAHIT.

The fertility conditions of the F_1-hybrids between synthetic and natural *Tetrahit* are of prime importance for judging the genotypical similarity of these types. In all F_1-hybrids obtained the percentage of good pollen was determined (table 5). The result was that all plants proved to be at least partially fertile, and a few plants had more than 90 per cent good pollen, thus showing complete fertility. Further it is evident that different lines of natural *Tetrahit* give different degrees of F_1-sterility. To take the extremes, the cross T—A $\times$ AT and reciprocally gave 14 F_1-plants with the average fertility 81,80 per cent; in the cross T—I $\times$ AT 10 F_1-individuals had on an average 47,50 per cent good pollen.

It is interesting that the nine different cross-combinations may be divided in two groups, one rather fertile with an average fertility ranging from 70,00 to 81,80 %, the other group being more sterile, with the averages ranging from 47,50 to 52,50 %. The former group comprises five cross-combinations, involving the pure lines T—A, T—B, T—D, T—E and T—M, the second group comprises four combinations, involving the lines T—C, T—F, T—I and T—N.

As previously reported on several occasions (1929, 1930 a, 1932) intraspecific sterility occurs in certain cross-combinations within *G. Tetrahit*. With certainty this sterility is due to the formation of lethal recombination gametes. Now, it may be surmised that the low fertility in the second group is in part due to some special factors in the *Tetrahit*-lines involved. This hypothesis is much supported by the following observations. The five pure lines mentioned above, which were involved in the relatively fertile cross-combination group, have been crossed *inter se* in seven different directions (MÜNTZING 1929, p. 309; 1930 a, pp. 229 and 231, and unpublished results). All the F_1-hybrids thus obtained (T—A × T—B, T—A × T—D, T—A × T—E, T—B × T—D, T—B × T—E, T—D × T—E and T—D × T—M) have been quite fertile. These lines have also been crossed with representatives of the second cross-combination group, and out of 10 combinations 7 proved to give partially sterile F_1-generations (T—A × T—C, T—A × T—F, T—B × T—C, T—B × T—F, T—D × T—C, T—E × T—I and T—M × T—C) whereas 3 combinations were fertile (T—D × T—F, T—E × T—C and T—E × T—F). Finally, two crosses within the second cross-combination group have been made, one giving a fertile F_1 (T—C × T—F), the other partial sterility (T—C × T—I).

The important fact is not, that some of the crosses between AT and *Tetrahit*-lines give better fertility than others. This is natural, and is to be expected from the frequent occurrence of intraspecific sterility in natural *Tetrahit*. *But the occurrence in some F_1-generations of quite fertile plants with 90—100 % good pollen shows that the genomes of synthetic Tetrahit may combine with those of natural Tetrahit without disturbances and without the formation of lethal recombination-gametes.* If in later generations the synthetic *Tetrahit*-types will be differentiated and stabilized, it is to be expected that some of the lines thus obtained will give fertile F_1-generations with natural *Tetrahit*, others partially sterile F_1-generations.

It may be mentioned that the fertile F_1-individuals obtained in the cross T—A × AT and reciprocally are with absolute certainty true hybrids. T—A has the inhibiting factor *H* and therefore the F_1-plants are dominant white. Two plants of the cross AT (♀) × T—A (♂) were dominant white and had 90—95 % good pollen. But from morphological details it was certain that also the reciprocal cross had given true hybrids. And in practically all other F_1-plants there were the same possibilities to demonstrate that the cross had been successful.

Concerning fertility in the F_1-hybrids under discussion, it may be

further remarked that no signs of anther deficiency were observed. Seed production seemed to be good and was in some plants quite as good as in pure lines of natural *Tetrahit*.

2. FERTILITY IN CROSSES BETWEEN AT AND BIFIDA.

The pollen fertility in five different F_1-combinations between AT and *bifida* was examined (table 5). All the plants proved to be partially sterile and more sterile than in the crosses between AT and *Tetrahit*. The average values range from 32,50 to 47,50 %. Crosses between *Tetrahit* and *bifida* always give partially sterile hybrids, the degree of sterility depending on the lines used and on environmental conditions (cf. MÜNTZING 1930 a, p. 241). Evidently, the AT-plant behaved like a true *Tetrahit* in the crosses with *bifida*. The seed production in these F_1-hybrids was also observed to be rather bad.

III. AN F_2-GENERATION FROM THE CROSS AT × T—A.

One seed from the cross AT × T—A was brought to germination in the autumn of 1930, and the seedling obtained was grown under electric light. A tiny plant was obtained which nevertheless flowered and set some seed. The plant was dominant white like the sister plants grown in the following summer and had on an average 65 per cent good pollen. Fortynine seeds were harvested, from which a small F_2-generation, consisting of 38 plants, was grown in the following summer. Though fragmentary, some of the results are of interest and may be briefly discussed.

Concerning flower colour 30 plants were dominant white (or yellowish white), 4 plants were redflowered, and 2 individuals had an aberrant type of flower colour (the buds slightly redbrown, the upper lip yellow, the side laps with a spot, the network running towards the edge).

Segregation in flower size was evident, and the variation in this respect and also in regard of height and other quantitative characters seemed to be greater than is generally the case in intraspecific *Tetrahit*-crosses. The pollen fertility was also investigated (table 5). Three of the plants had in part defective anthers containing rather bad pollen, the pollen percentage being 8, 38 and 48 resp. These plants were also markedly small-flowered. Probably this coincidence is causal and the phenomenon analogous to the occurrence of small-flowered, »female» plants in other *Galeopsis*-crosses (1930 a, p. 306). The seed production

indicated that these three plants had good female fertility. The pollen fertility of the F_2-plants, including the three plants with defective anthers, varied continuously within the limits 5—95 per cent, which is a type of variation seldom found in intraspecific *Tetrahit*-crosses (cf. however 1932, p. 91).

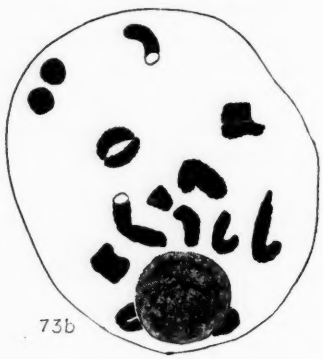
If any conclusions are to be drawn from the present preliminary material, they should be the following. Segregation is more profound than in most line crosses within *G. Tetrahit* but not so transgressive as in the *Tetrahit* × *bifida*-crosses (cf. 1930 a, pp. 258—270). Segregation products appear which are »unbalanced», having defective anthers and small flowers. The variation of pollen fertility is not of the kind generally found in partially sterile *Tetrahit*-crosses. This may be due either to somatic influences or to recombination of many but small factorial differences which influence the viability of the haplophase. This will be further investigated. Other F_1-plants may give different results in the following generations.

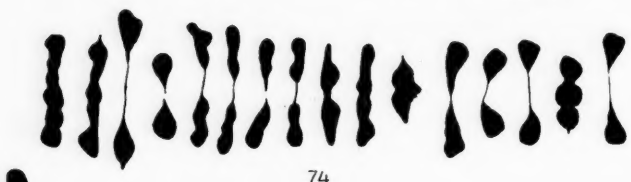
CYTOLOGICAL INVESTIGATIONS.

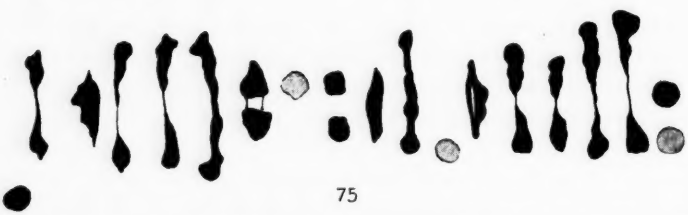
I. SOMATIC CHROMOSOMES.

Root tips from all plants belonging to the I_1-generation and from some of the hybrids between AT and *Tetrahit* and *bifida* were fixed. The fixatives used were KARPECHENKO's modification of NAWASCHIN's solution, which gave good results, and LA COUR's fixative 2 BE (LA COUR 1931) which for this material proved to be quite useless. The sections were cut about 16 μ and stained with gentian violet.

Up to this date the chromosome numbers of 33 I_1-plants have been determined with the following results. Twentyfour plants had $2n = 32$ like the mother plant, AT, 4 plants had $\pm$ 32 chromosomes, and 5 individuals had $2n = 33$. Thus, the majority of the plants have the normal chromosome number 32, a few plants have got an extra chromosome. Somatic plates from two of the trisomic plants are represented by figs. 71 and 72. In fig. 72 some of the chromosomes are rather short; thus it may be possible that in this plant the increase in chromosome number is due to fragmentation of one chromosome. However, in another trisomic plant the aberrant number was also controlled at the reduction division (cf. below, p. 127). Thus it is certain that true trisomics were produced in the progeny of the primary tetraploid. It is interesting that, hitherto at least, no monosomic plants with 31 chromosomes have been found.







Figs. 71—72. Somatic chromosomes from two trisomic I_1-plants ($2n = 33$). — Figs. 73—75, meiosis in a trisomic I_1-plant. Fig. 73, diakinesis (in two sections); fig. 74, heterotype metaphase (side view, $16_{II} + 1_I$, separately drawn); fig. 75, heterotype metaphase ($14_{II} + 5_I$). — Magnification: figs. 71—72, 2650 ×, figs. 73—75, 3375 ×.

In fig. 71 four or five satellites are visible. Satellites have been observed now and then and also in the diploid species (cf. 1930 b, fig. 11). On account of the smallness of the chromosomes they are often difficult to distinguish and their number in the diploid and tetraploid species has not yet been determined with certainty. It may be mentioned, however, that satellites have been observed also in natural *Tetrahit*. One somatic plate from a plant belonging to the line T—C showed four chromosomes with satellites.

In fig. 72 attachment constrictions are visible in some of the chromosomes. Some of them are evidently median, others subterminal. Better methods of fixation and staining may perhaps further elucidate the chromosome morphology in *Galeopsis*, though this material is certainly not favourable for such studies.

Besides studies of the I_1-generation, five F_1-hybrids between AT and *Tetrahit* and one hybrid between AT and *bifida* were controlled and found to have 32 somatic chromosomes. Studies of the reduction division, however, showed that another F_1-hybrid from the cross AT (♀) × T—D (♂) was trisomic (cf. below, p. 133).

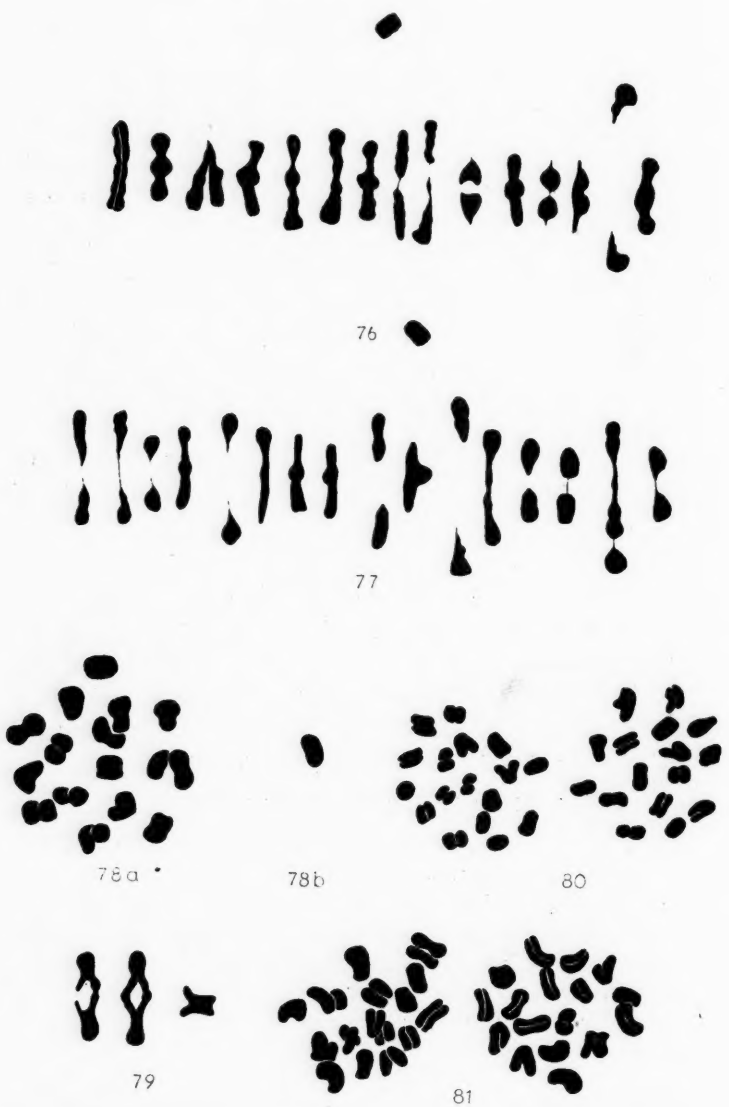
II. MEIOTIC DIVISIONS.

Flower buds for studies of the reduction division in the pollen mother cells were fixed in various fixatives. The material now represented was fixed in CARNOY for some minutes and then brought into KARPECHENKO's fluid (the same as used for the root tips). Sections were cut 16—18 μ and stained with gentian violet.

1. MEIOSIS IN A TRISOMIC I_1-PLANT.

The I_1-plant 1931—200—18 was found to have 33 somatic chromosomes, which number was verified by studies of the reduction division. — Figs. 73 *a* and *b* represent the chromosomes at diakinesis (two sections). Though the chromosome configurations are in part obscure, there are probably no multivalents. Some clear bivalents are visible, which are either united end to end or ringshaped with two terminal chiasmata. Some of the chromatine bodies must be univalents, but bivalents and univalents can not be distinguished with certainty.

Figs. 74—77 show four complete chromosome complements of the heterotype metaphase (side view, separately drawn). The typical case (fig. 74) is the occurrence of $16_{II} + 1_I$, the univalent lying more or less apart from the other chromosomes. In some cases more than one uni-



Figs. 76—81. Meiosis in a trisomic I_1-plant (continued). — Fig. 76, heterotype metaphase ($14_{II} + 2_I + 1_{III}$); fig. 77, heterotype metaphase ($15_{II} + 1_{III}$); fig. 78, heterotype metaphase, polar view in two sections ($16_{II} + 1_I$); fig. 79, two bivalents, showing

valent was observed. Fig. 75 shows $14_{II} + 5_{I}$. More rarely trivalents are formed as in fig. 76 where the chromosome complement consists of $14_{II} + 2_{I} + 1_{III}$. Fig. 77 shows $15_{II} + 1_{III}$. In the former case the trivalent has the shape of a V with a rod at each arm, in the second case it is a triple chain. The number of univalents was determined in 18 cases. The numbers found were: 0 (3 cases), 1 (12 cases), 2 (1 case) and 5 (2 cases). Probably then, the configuration represented in fig. 74 with $16_{II} + 1_{I}$ is the most frequent. It is to be noted that quadrivalents were not observed in this plant, neither in side view nor in polar view (fig. 78). Fig. 78 shows $16_{II} + 1_{I}$ in two sections.

At the heterotype metaphase the bivalents are generally associated by one terminal chiasma, seldom by two (as in fig. 75, no. 6 from the left and fig. 76, no. 6 from the right; cf. also MÜNTZING 1932, fig. 2, p. 96). The chromatid structure was sometimes clearly visible (fig. 79).

At the heterotype anaphase 16 chromosomes pass to one pole, 17 to the other (figs. 80 and 82). This distribution was very regular, and lagging chromosomes were seldom observed. The univalents pass undivided to the poles. Only in one case (fig. 79), a univalent lying in the equatorial plane at early anaphase showed a tendency to split. Of 32 P. M. C. in interphase 27 were normal in appearance, 5 showed micronuclei. At the homotype metaphase, chromosomes were observed to be eliminated in 8 cases, whereas conditions were normal in 39 cases. The chromosome number could be counted in seven homotype metaphase plates, showing 4 plates with 16 and 3 plates with 17 chromosomes (cf. fig. 81).

2. MEIOSIS IN NORMAL I_1-PLANTS.

Some slides were also obtained from I_1-plants with the normal chromosome number 32. Figs. 83—87 show meiotic divisions in the plant 1931—200—29, fig. 88 is from another I_1-plant (1931—200—26).

One heterotype metaphase in side view showed quite regularly 16_{II} (fig. 83). In another metaphase in polar view (fig. 84) there seems to be $14_{II} + 1_{IV}$. The quadrivalent, however, may be suspected to consist of two bivalents lying close together but without exchange of chromatids.

Fig. 87 shows a starting heterotype anaphase. In all there are 32 chromosomes, but it is uncertain, how these will be distributed. In this plant micronuclei at interphase were not unusual (fig. 85). In all 138

chromatid structure and terminal chiasmata, and one univalent with tendency to split; fig. 80, heterotype anaphase (polar view, in one section), showing the distribution 16—17; fig. 81, homotype metaphase in one P. M. C. (polar view), showing the distribution 16—17. — Magnification: 3375 ×.

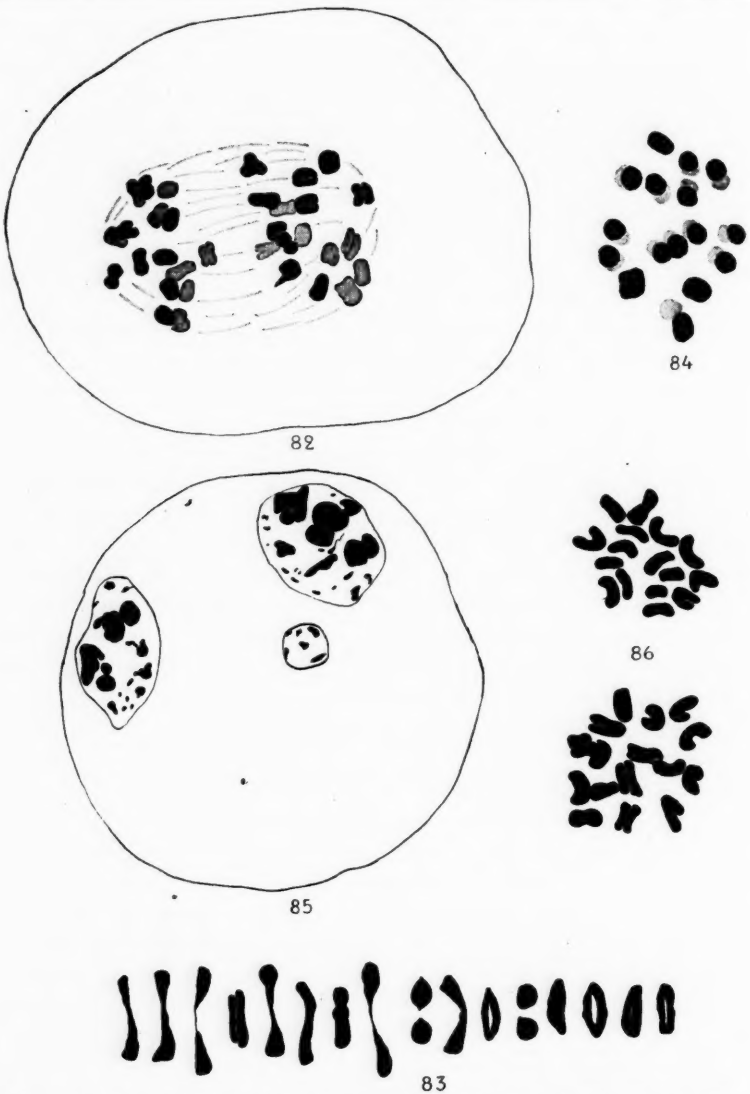
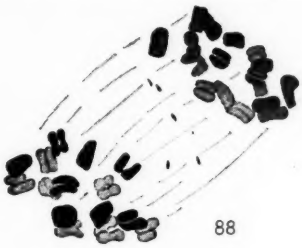


Fig. 82. The trisomic I_1-plant; heterotype anaphase, side view, showing the distribution 16—17. — Figs. 83—86. Meiosis in the normal I_1-plant 200—29. Fig. 83, heterotype metaphase, side view, (16_{II}); fig. 84, heterotype metaphase, polar view, ($14_{II} + 1_{IV}$ or 16_{II}); fig. 85 interphase with one micronucleus; fig. 86, homotype metaphase ($16 + 16$ from one P. M. C.). — Magnification: Fig. 85, 2250 ×, the other figures, 3375 ×.

87



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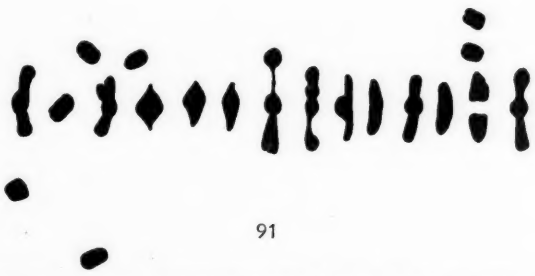
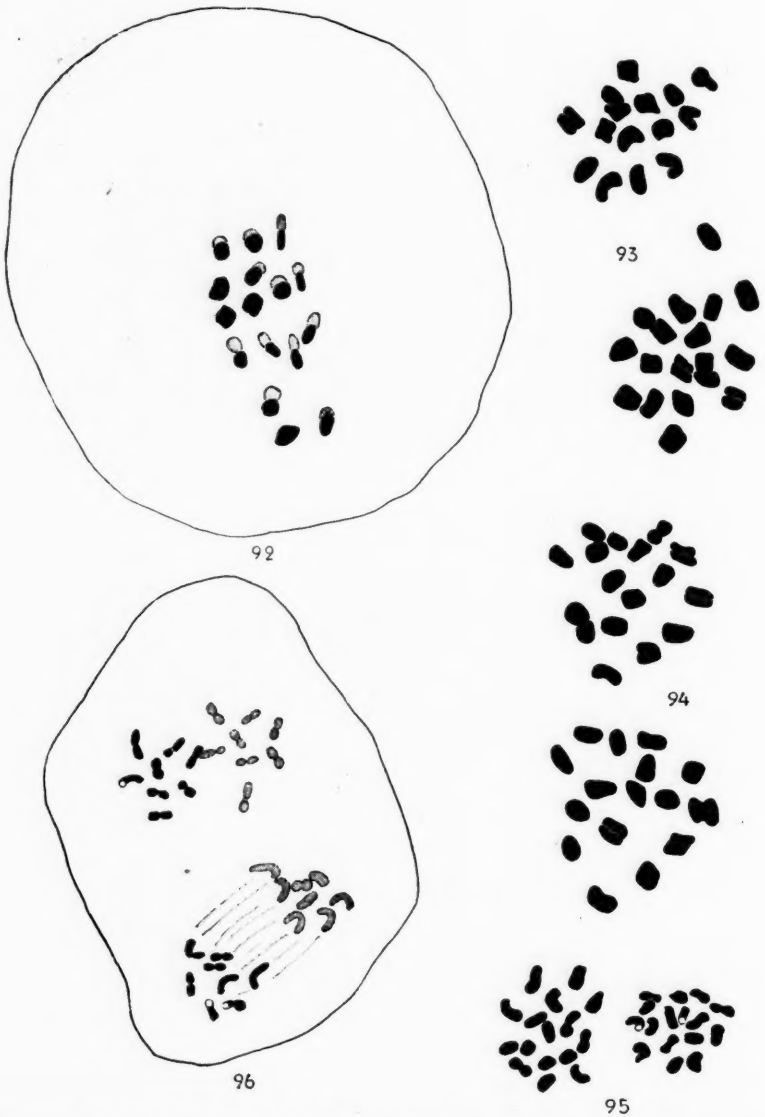


91

Fig. 87. Heterotype meta-anaphase from the I_1-plant 200—29, (side view, in all 32 chromosomes). — **Fig. 88,** heterotype anaphase from another I_1-plant, 200—26, showing the distribution 15—17. — **Figs. 89—91.** Meiosis in a trisomic hybrid between natural and synthetic *Tetrahit*; heterotype metaphase in side view (separately drawn). — **Fig. 89,** $15_{II} + 1_{III}$; **fig. 90,** $15_{II} + 1_{III}$ (no. 3 from the right); **fig. 91,** $13_{II} + 7_{I}$. — Magnification: 3375 ×.



Figs. 92—94. Meiosis in a trisomic F_1-plant (continued). Fig. 92, heterotype metaphase, polar view; fig. 93, heterotype anaphase (polar view, in one section), showing the distribution 15—18; fig. 94, the same, but the distribution is 16—17. — Fig. 95,

P. M. C. from two slides were examined. Of these 20 cells, that is about 14 per cent, showed micronuclei. At the homotype metaphase obviously eliminated chromosomes were also observed. Fig. 86, however, represents a homotype metaphase with the normal distribution 16 + 16.

In fig. 88 a heterotype anaphase from the plant 1931—200—26 is represented. The distribution is here evidently 15—17 instead of 16—16. — In this plant chromosome elimination must have been rare. Out of 100 P. M. C. in interphase only 2 had micronuclei.

3. MEIOSIS IN HYBRIDS BETWEEN NATURAL AND SYNTHETIC TETRAHIT.

Some good preparations were obtained from a trisomic plant ($2n = 33$) of the cross AT (♀) × T—D (♂). In all essentials the chromosome behaviour was as in the trisomic I_1-plant. Thus, *the chromosomes of synthetic Tetrahit find homologues among the chromosomes of natural Tetrahit.* Figs. 89 and 90 show heterotype metaphases with $15_{II} + 1_{III}$. Sometimes a varying number of univalents was observed. Fig. 91 represents an extreme case with $13_{II} + 7_{I}$. There was no indication of larger associations than trivalents. In fig. 92, heterotype metaphase in polar view, 16 separate bodies are visible, of which 12 are evidently bivalents. One of the remaining bodies is probably a trivalent. In another case, not figured, the chromosome complement consisted of $15_{II} + 3_{I}$. Two heterotype anaphases were observed (figs. 93 and 94), where the chromosome distribution was 15—18 and 16—17 respectively. Of 53 P. M. C. in interphase 41 were normal in appearance, 12 showed eliminated chromosomes or micronuclei.

One hybrid between AT and the *Tetrahit*-line T—M had probably the normal chromosome number 32 and a rather regular reduction division, according to absence of eliminated chromosomes. In the homotype anaphase the distribution 16—16 was observed (fig. 95).

In previous publications (MÜNTZING 1927; 1930 a, pp. 289—290; 1930 b, pp. 158—160) I have shown that chromosome number and size of nuclei, pollen mother cells and pollen grains are correlated in *Galeopsis*. Obviously the synthetic *Tetrahit*-plants have also bigger pollen mother cells than the original parents. For comparison with the other chromosome pictures, a pollen mother cell from one of the parents, *pubescens*, is represented by fig. 96. The eight chromosomes are visible

homotype anaphase from another F_1-plant between natural and synthetic *Tetrahit* (polar view in one section, showing 16 + 16 chromosomes). — Fig. 96, *G. pubescens* (the parental biotype). Homotype anaphase ($n = 8$). — Magnification: 3375 ×.

in all of the four homotype anaphase plates, and the size of the cell is smaller than in the tetraploid types.

MORPHOLOGY AND FERTILITY OF THE TRISOMIC PLANTS.

Among the I_1-plants five trisomic individuals were found (cf. p. 125). As to morphology, two of these plants were aberrant. One of them was a dwarf plant with abnormal leaves but normal flowers of *Tetrahit*-type (fig. 40). The other one, 1931—200—18, was vigorous and vegetatively well-proportioned but remembered more of *pubescens* than the other I_1-plants. Further it was conspicuously big-flowered (figs. 48 and 64), and had aberrant flower shape and network. The other three plants with an extra chromosome were morphologically typical *Tetrahit*-plants. One of those latter had somewhat defective anthers, containing 36 per cent good pollen. The other four plants had a pollen percentage ranging from 59 to 69.

Evidently, the occurrence of I_1-plants with an extra chromosome has to some degree increased the morphological variation and decreased the average fertility.

The trisomic hybrid, obtained in the cross between AT and the *Tetrahit*-line T—D (cf. p. 133) died before flowering and was not morphologically examined.

DISCUSSION.

I.

From reasons given in detail in previous papers (MÜNTZING 1930 a, p. 295; 1930 b, pp. 160—163) the genotypical constitution of the AT-plant must have been $\frac{p\,s}{p\,r}$, where p symbolizes the *pubescens*-genome, s the *speciosa*-genome, and r a recombination-genome, containing genes from both of the parental species. At the reduction division of AT it is probable that the two *pubescens*-genomes have formed eight bivalents and the *speciosa*- and recombinations-genome also eight bivalents. In the latter case the pairing may have been partly loose, as in the F_1-hybrids, *pubescens* $\times$ *speciosa*, besides regular conjugation a varying number of univalents may be formed (1930 a, pp. 285—287). However, in the AT-plant the divisions in the P. M. C. seemed to be quite regular (1930 b, p. 159). It was therefore assumed that the partial pollen sterility observed in this plant was due to heterozygosity (s—r) and scarcely to chromosome irregularities. This conclusion has been criticized by KIHARA (1931 a) who

believes (p. 153) that the genome interpreted by me as recombination-genome »ausschliesslich (oder fast ausschliesslich) aus den Gliedern des *S*-Genoms besteht». If this were correct the sterility would be due to chromosome irregularities, not to heterozygosity. However, from several reasons it is probable that the *r*-genome is really a recombinationgenome.

In F_2 of the cross *pubescens* × *speciosa* a multitude of different diploid plants were obtained (1930 a, pp. 282—285). Obviously then, recombination-gametes must be frequent and functional, and the triploid F_2-plant, pseudo-*Tetrahit*, is therefore most probably the result of a union between one unreduced gamete carrying the complete *pubescens*- and *speciosa*-genomes and one recombination-genome. Secondly, if the constitution of the AT-plant had been $\frac{p\,s}{p\,s}$ it ought to have been morphologically very similar to the diploid hybrid $\frac{p}{s}$. That was not the case (1930 a, pp. 291—293). Thirdly, the morphological diversity of the I_1-generation is, no doubt, the expression of a corresponding genotypical diversity. Consequently, the mother plant must either have been heterozygous or have formed viable gametes of many different kinds due to frequent irregularities of the reduction division. It is true that in the progeny some trisomic plants with one extra chromosome were obtained. This shows that the meiotic divisions in the primary tetraploid have not been quite regular at least in the ovules. This fact may in part explain the partial sterility observed. But nevertheless it is probable that the multitude of different I_1-forms with normal chromosome number are chiefly the result of recombination, not of chromosome irregularities. The I_1-results in combination with the other facts may therefore be considered a verification of the previous deductions concerning the genotypical constitution of the synthetic *Tetrahit*-types. This view is also supported by the fact that all I_1-plants were redflowered as demanded by the theory. If chromosome distribution is regular, each gamete must contain one *pubescens*-chromosome, carrying the redfactor, since the AT-plant was assumed to have two *p*-genomes, forming eight bivalents at the reduction division. Possibly the *r*-genome also contains a redfactor, since the nuance and intensity of red was variable in I_1.

Considering the experimental formation of allo-polyploids in general, these types with an increased chromosome number have been produced or observed to arise in several different ways.

In a few cases the doubling of the chromosomes has taken place during the somatic development, either spontaneously as in *Primula Kewensis* (see NEWTON and PELLEW 1929) and *Nicotiana digluta* (CLAUSEN and GOODSPEED 1925, R. E. CLAUSEN 1928) or by special methods, as in *Solanum nigrum* × *luteum* (JØRGENSEN 1928) and certain moss hybrids (WETTSTEIN 1924). In the majority of cases, however, the chromosome increase is due to the formation of unreduced gametes.

1) Chiefly as the result of »restitution» (ROSENBERG 1917, 1927) or »regression» (KIHARA 1931), sometimes in other ways, F_1-gametes with the somatic chromosome complement may be formed. The union of such gametes will give riso to »amphidiploids» (NAWASCHIN 1927) already in F_2. To this type the following cases belong: *Raphano-Brassica* (KARPECHENKO 1927, 1928, 1929), *Aegilotricum* (KIHARA 1931 a, probably also the case first described by TSCHERMAK and BLEIER 1926 and that of PERCIVAL 1930), *Digitalis Mertonensis* (BUXTON and NEWTON 1928; BUXTON and DARLINGTON 1931), *Nicotiana rustica* × *paniculata* (SINGLETON 1928; LAMMERTS 1929, 1931), *Saxifraga Potternensis* (WHYTE 1930), *Fragaria Helleri* × *bracteata* (ICHIJIMA 1930), probably also the *Phleum*-case (GREGOR and SANSOME 1930).

Viola hyperchromatica (CLAUSEN 1924, 1926), which shows a partial increase of chromosome number, arose from the cross *V. tricolor* × *arvensis* after splitting of some univalents in both meiotic divisions.

It should be observed that unreduced gametes may be formed even in hybrids where chromosome conjugation is good. Non-conjunction due to lacking affinity is no necessary presumption for the origin of gametes with a somatic complement. *E. g.* in the hybrid *Nicotiana rustica* × *paniculata* (LAMMERTS 1929, 1931) the chromosome pairing is good, but nevertheless about 30 per cent of the ovules are unreduced. Similar conditions are met with in the *Saxifraga* case (WHYTE 1930).

2) In other, less extreme cases, where reduced gametes are formed and function, such gametes may unite with unreduced ones, and give rise to allo-triploids. Such was the origin of the triploid pseudo-*Tetrahit*-plant. Quite analogous cases have been found in the *Salix*-crosses of HERIBERT NILSSON. Several F_2-plants of the cross *S. caprea* × *viminalis* had an increased chromosome number (HÅKANSSON 1929 a). One »gigantea»-plant was found to be triploid, another F_2-plant, »*neocinerea*» (HERIBERT NILSSON 1931), was probably triploid or hypertriploid. In F_2 of the cross *Nicotiana rustica* × *paniculata* the majority of the plants were allo-tetraploid, but a few triploid plants were also obtained, since also a minority of reduced gametes are functional in F_1.

3) In some other cases, where F_1 has been back-crossed to the parents or other types, unreduced F_1-gametes have caused an increase of chromosome number in the progeny. Such was the case in the cross *Nicotiana tabacum* × *Rusbyi* (BRIEGER 1928, 1930), where F_1 was back-crossed to *tabacum* and to *silvestris*. An analogous case was obtained by YARNELL (1931) in the cross *Fragaria* (*vesca* × *Chiloensis*) × *Chiloensis*.

4) Finally, we have those cases where the chromosome increase is obtained already in F_1, due to the formation of unreduced gametes by one of the parents, as *e. g.* in the crosses *Rubus rusticanus inermis* × *R. thyrsiger* (CRANE and DARLINGTON 1927), *Euchlaena perennis* × maize (EMERSON and BEADLE 1930) and *Nicotiana tabacum* × *rustica* (EGHIS and RYBIN, according to RENNER 1929). The latter case is especially interesting, as the triploid F_1-plant, when back-crossed to *rustica*, gave an allo-tetraploid descendant with probably two *rustica*- and two *tabacum*-genomes. This plant was fertile and showed 48 bivalents at the reduction division. — This case is somewhat similar to the *Galeopsis*-results. However, the triploid *Galeopsis*-plant appeared in F_2, not in F_1, further it contained a recombination-genome, which caused the primary tetraploid to be heterozygous. And in next generation this heterozygous plant gave rise to a swarm of different types.

II.

The chromosome behaviour at the reduction division of an allo-polyploid is to a certain extent correlated with the mode of chromosome pairing in the diploid original hybrid. If there is non-conjunction or weak affinity between the different genomes of the parent species, this is a guarantee that the meiotic divisions in the allo-polyploid will not be much disturbed by multivalent formation or interspecific pairing. Such typical conditions are found in *Raphano-Brassica, Nicotiana digluta* and *Aegilotricum*. But even in these cases the reduction division does not seem to be quite regular. Sometimes there are minor irregularities, lagging chromosomes, microcytes etc. In the *Aegilotricum*-case studied by KIHARA (1931 b) the primary hybrid shows 0—6 »lockere Bindungen». In the allo-tetraploid there are generally 28 bivalents but sometimes slight disturbances, which may lead to the formation of gametes with deviating chromosome numbers. Crosses with *Triticum spelta* showed that *Aegilotricum*-gametes with 27 chromosomes instead of 28 are formed and function.

Turning to the opposite extreme as represented for instance by the cross *Crepis rubra* × *foetida* (POOLE 1931), the pairing in the diploid

F_1-hybrid is good. In the amphidiploid derivative, obtained in F_2, quadrivalent formation is frequent and sometimes complete (five quadrivalents, corresponding to the five bivalents in F_1).

However, several cases are known where the chromosome conjugation in the primary hybrid is good, and nevertheless meiosis in the allotetraploid in the main regular. Such is the case in the cross *Solanum nigrum* × *luteum* (JØRGENSEN 1928), in the *Saxifraga*-case (WHYTE 1930) and in *Primula Kewensis* (NEWTON and PELLEW 1929). In the latter case, however, one, seldom 2—3, quadrivalents are usually formed in addition to the bivalents.

In *Galeopsis* the primary hybrid, *pubescens* × *speciosa*, was observed to form eight bivalents at the heterotype metaphase, but not seldom there was non-conjunction in some pairs leading to the formation of a varying number of univalents. Thus, the affinity between the *pubescens*- and *speciosa*-genomes may be considered relatively good though evidently in part diminished.

In the triploid F_2-plant, containing one *speciosa*-, one *pubescens*- and one recombination-genome, trivalents were not rare (1930 a, pp. 287—289) which is in accordance with expectation. In the tetraploids (the I_1-generation) regular pairing is evidently the rule. Sure quadrivalents were not observed, neither in plants with 32 chromosomes nor in the trisomic individual investigated (cf. above, pp. 127—133). On the contrary, partial non-conjunction may sometimes occur, leading to the production of some univalents. Absence of quadrivalents in *Galeopsis* and the other cases described above where pairing in the diploid hybrid was good, may be caused by two circumstances.

Firstly, it is probable that pairing between like chromosomes, derived from the same species, prevails. In *Galeopsis*, for instance, the affinity between the *pubescens*- and *speciosa*-genomes is somewhat weak. Therefore intraspecific pairing $\left(\frac{p}{p}\right)$ is more likely to occur than interspecific $\left(\frac{s}{p}\right)$, in cases where there is opportunity for both ways as in the allo-tetraploids.

Secondly, absence of quadrivalent formation may be due to mechanical causes, viz. low frequency of chiasmata. It has been shown (cf. DARLINGTON 1931) that chromosome pairing in the strict sense is due, not to affinity between the chromosomes as entities, but to affinity between chromatids and the formation of chiasmata during the meiotic prophase. High frequency of chiasmata will favour the formation of

multivalents and *vice versa.* In *Galeopsis* the chromosomes at the heterotype metaphase are generally united by one terminal chiasma, seldom by two. This low chiasma frequency may in part be responsible for the absence of quadrivalents and the regular occurrence of bivalents in the allo-tetraploid *Galeopsis*-plants. It also agrees with the occasional formation of trivalents in the triploid and trisomic plants examined. In the polyploid species *Dahlia variabilis* LAWRENCE (1931) has observed »secondary association» of chromosomes, which is supposed to be due to a general affinity between more than two chromosomes. This results in their juxtaposition at first metaphase. This phenomenon is distinct from true multivalent formation by means of chiasmata. LAWRENCE has the opinion that such secondary association should occur in all allo-polyploids. In the present *Galeopsis*-material the bivalents at first metaphase were sometimes lying close together. Further observations may decide whether this is only incidental or due to the same phenomenon as in *Dahlia.*

The primary allo-tetraploid, AT, had the constitution $\frac{ps}{pr}$. Most I_1-plants will be somewhat different from the mother plant, due to recombination between the *s*- and *r*-genomes. The univalent formation observed may either be the result of lacking affinity between *speciosa*-chromosomes and *pubescens*-chromosomes, derived from the *r*-genome, or the result of a simultaneous trivalent-formation. Non-conjunction may also be caused by somatic influences, the occurrence of which may be suspected especially in the trisomic plants. *E. g.* in tri- and monosomic forms of *Nicotiana alata* (GOODSPEED 1931) there is a strong tendency to non-conjunction.

Multivalent formation at first metaphase may be the cause of subsequent irregularities. If the chromosomes are associated by means of terminal chiasmata, separation at anaphase will be easier than in cases of interstitial chiasmata (cf. LAWRENCE 1931). In both cases the distribution of chromosomes to the poles may be unequal, but in plants with terminal chiasmata, there is less risk of delayed separation and lagging chromosomes and hence less risk of chromosome elimination. — In *Galeopsis*, where the chiasmata are terminal, the divisions are also generally clean. Such was the case in the triploid (1930 a, p. 289) and also in the trisomic plants described above. However, in some plants micronuclei at interphase were not rare. This is evidently not caused by multivalent formation but on the contrary by non-conjunction and scattered univalents.

III.

Fertility in allo-polyploids is very much influenced by the course of the meiotic divisions. The *Crepis* amphidiploid just mentioned had a high degree of multivalent formation and not more than 35 per cent of good pollen. In other cases with more regular reduction, fertility is also better and sometimes very good. But compared with the parent species fertility in allo-polyploids is generally not quite first-class at least in the first generations after their origin. In some cases, however, there seems to be a tendency to stabilization in later generations, as in *Saxifraga* (WHYTE 1930) and in the *Nicotiana rustica* × *paniculata*-case (LAMMERTS 1931). Allo-polyploid *Aegilops-Triticum* hybrids were first obtained by TSCHERMAK (TSCHERMAK and BLEIER 1926) and later by PERCIVAL (1930) and KIHARA. KIHARA (1931 b) finds that his newly arisen *Aegilotricum*-forms are less fertile than the relatively old strains of TSCHERMAK. This may possibly be due to increasing fertility in later generations. (Interactions between chromosomes and plasma?).

In the *Galeopsis*-case we must assume that in the primary allo-tetraploid, part of the sterility was caused by heterozygosity. Contrary to most other cases this plant did not contain just two genomes of one sort and two genomes of another. Therefore in next generation (I_1) a wide range of fertility variation was obtained (table 5, p. 119). Especially interesting is the fact that about 40 per cent of the I_1-plants had better fertility than the mother. One plant had even more than 90 per cent good pollen. Therefore, further segregation products with full fertility may be expected in future generations.

Among the I_1-plants sterility phenomena were also observed, obviously of diplontic character and caused by the mother plant, viz. deficient anthers and lumped pollen grains. Also in other allo-polyploids there are indications of diplontic sterility. In the amphidiploid *Solanum nigrum* × *luteum* reduction division is normal, but only 35 per cent of the pollen is good (JØRGENSEN 1928). In the *Raphano-Brassica* case a small part of the tetraploids, notwithstanding regular meiosis and normal pollen, proved sterile or of reduced fertility. This was more frequent when a certain variety of *Brassica oleracea* was used for the cross (KARPECHENKO 1928).

IV.

It is typical for allo-polyploids that in contrast to the original F_1-generation they are fertile and morphologically constant. As a rule, however, constancy as well as fertility is not absolute due to unstable

meiosis. In the progeny from *Digitalis Mertonensis*, $^1/_4$ of the plants are less fertile than the rest, in the progenies from *Aegilotricum* and *Primula Kewensis* a small proportion of the descendants have slightly aberrant chromosome numbers (tri- and monosomic types etc.). Morphological variation may also be caused by interspecific pairing, without changes in chromosome number (as in *Primula Kewensis*). Some degree of polymorphism may also be the result when allo-polyploids are obtained from several F_1-plants with slightly different genotypical constitution, as is the case in *Raphano-Brassica* (KARPECHENKO 1928).

In all these cases, however, the variation is rather limited, at least in the generations next after the origin. The *Galeopsis*-case is unique in the respect that the primary tetraploid in the next generation gave rise to a swarm of different types. The differences between these plants though relatively slight, affect all of the morphological characters observed (height, flower dimensions, flower colour, type of network, calyx size, leaf shape, hairiness etc.). *An allo-polyploid population of this kind probably represents a more favourable material for natural selection than those allo-polyploids which from the beginning are constant or relatively constant.*

V.

A characteristic feature of auto-polyploids is their vegetative vigour, which is often striking enough to be called gigantism. This gigantism may be due to two different causes which are both a consequence of the chromosome doubling: 1) increase of cell volume, 2) doubling of the genes, influencing quantitative characters (cf. MÜNTZING 1931 b). — As a rule allo-polyploids are also more vigorous than the parents, but the gigantism is on an average less pronounced than in cases of auto-polyploidy. Among 14 different cases of allo-polyploidy 12 cases were found to show gigas-characters in one or another respect (cf. MÜNTZING 1931 b, p. 9). In part this gigantism may result from maintenance of hybrid vigour, as a polyploid which is the result of doubling in a cross between dissimilar forms will be heterozygous in all respects in which its parents differed (DARLINGTON 1928, HUSKINS 1931 a and b). The cause may also be more mechanical and due to increased cell volume.

Correlation between gigantism and increase of chromosome number is interpreted in another way by HERIBERT NILSSON (1930 a). In F_2 of the cross *Salix caprea* × *viminalis* a triploid gigantea-plant was obtained. HERIBERT NILSSON says (l. c. p. 77): »Es ist wahrscheinlich in diesem Falle gerade die erwartete extreme Rekombination von Fak-

toren für Blattgrösse, die morphologisch riesengross ausfallen muss, welche auch gleichzeitig eine vermehrte Chromosomenzahl verursacht». However, this interpretation is opposed by the following facts. In *Spirogyra* GERASSIMOFF and VAN WISSELINGH (see VAN WISSELINGH 1920) have obtained doubling of chromosome number by means of different external influences. Such altered *Spirogyra*-threads which also arise under natural conditions are typical gigas-types in comparison with the original forms. It is quite clear in this case that the chromosome doubling is induced by the experimental treatment and that the alteration of the morphological characters is a result of the chromosome doubling. This is equally clear in WETTSTEIN's experiments on mosses (WETTSTEIN 1924). Regeneration of cells from the diploid moss capsule gives diploid protonemata and diploid gametophytes, which are gigas-types in comparison with the original haploid gametophytes. Most probably the same arguments may be applied also to cases in higher plants. *E. g.* in *Epilobium hirsutum* MICHAELIS (1928) succeeded in producing unreduced pollen grains after cold treatment. These unreduced pollen-grains were picked out and used for pollination, which resulted in triploid »semigigas»-plants. Hence it is logical to assume, that also in other cases morphological gigantism is caused by chromosome doubling. Sure enough, special genetic factors or genetic combinations may result in morphological gigas-characters, but it is difficult to understand how these combinations should also be able to induce a simultaneous increase of chromosome number.

Concerning the morphology of the allo-polyploid *Galeopsis*-plants, the height variation has been discussed above (p. 107). On an average the I_1-plants were probably more vigorous than the original parents. This gigantism, however, does not affect flower size. On the contrary, in this case the allo-tetraploids have much smaller flowers than the parents (table 2). This calls for a special explanation.

It was found (1930 a, table 31, p. 282) that in F_2 of the cross *pubescens* × *speciosa* the average flower length ($22{,}68 \pm 0{,}27$ mm.) was considerably smaller than that of the parents ($29{,}34 \pm 0{,}20$ and $27{,}08 \pm 0{,}44$ mm. resp.). Small-flowered F_2-plants were segregated, and the variation was transgressive mainly to the minus side. — *G. speciosa*, at least the biotype used for the cross, is a cross-fertilizer, though seed may be obtained on artificial selfpollination. In *G. pubescens* seed production on isolation is relatively good and anyhow better than in *speciosa*. Probably however, also this species has a marked tendency to cross-fertilization (cf. 1930 a, p. 189). In view of these facts it is possible

that the big flowers in *speciosa* and *pubescens* represent a genotypical adaptation to cross-pollination, and that therefore these species represent extreme combinations with regard to the genes which affect flower size. After crossing the result in F_2 will be a majority of less extreme combinations which are relatively small-flowered (cf. 1930 a, table 31). The triploid F_2-plant was also rather small-flowered (17,07 mm. [1930 a, p. 291]). The daughter plant, AT, which differed genotypically from the mother by having one more *pubescens*-genome, had somewhat larger flowers (19,86 mm. [1930 b, p. 154]). In the following generation, I_1, there was a good deal of variation (table 2, p. 108), but the average (19,23 $\pm$ 0,21 mm.) was about the same as in the mother plant.

The natural tetraploid species, *Tetrahit* and *bifida,* are small-flowered and autogamous (1930 a, p. 188) but after interspecific crossing big-flowered transgressions may be obtained (1930 a, p. 267). Therefore, it seems very probable that the small flower size is an adaptation to autogamy. Then, the question rises: why are the diploid species cross-pollinating, the tetraploid ones autogamous? As is well-known, selfsterility seems to be generally controlled by systems of multiple allelomorphs which regulate the interactions between pollen tubes and styles. Pollen cannot function in the style of a plant carrying the same factors as the pollen itself. As pointed out by LAWRENCE (1930), self-sterility behaviour is different in diploids and polyploids, and to a certain extent the selfsterility mechanism may be disturbed by chromosome doubling. For instance, in diploids, S_2-pollen will not grow in S_1S_2-styles, but in a tetraploid, S_1S_3-pollen may perhaps be able to function in $S_1S_1S_2S_2$-styles. The greater number of possible combinations in polyploids will on an average make such plants more selffertile than diploids.

It is not certain if these arguments can be applied to the *Galeopsis* case, as selfsterility factors are not known in the diploid species *pubescens* and *speciosa.* But it is possible — and this will serve as a working hypothesis — that the cross-fertilization in these species is favoured by selfsterility factors with a rather weak effect (not preventing success of artificial selfpollination). In the tetraploids the selfsterility mechanism may be still weaker and unable to prevent spontaneous autogamy.

Experimentally produced polyploids are generally more vigorous than the diploid parents. The question is whether the same correlation between chromosome number and vigour is found among wild plants? Increase of chromatine mass leads to increased size of nuclei and cells. But

as the size of the vegetative organs depends on two variables, cell size and cell number, it is not certain that high chromosome numbers are always correlated with vegetative vigour. Whether the cell number is altered or not, may be approximately judged by countings of the number of pollen mother cells in sections of the anther lobes (JARETZKY 1928, p. 455 ff.). In certain plant groups, as for instance the family *Polygonaceæ*, there is a strong correlation between chromosome number and vegetative vigour. In *Rumex* the chromosome number may be approximately estimated according to the size of flowers and fruits (JARETZKY 1928). Among some *Potentilla*-species there also seems to be a certain proportionality between chromosome number and size of plants (MÜNTZING 1931 a). The same correlation is found among viviparous forms of *Festuca ovina* (TURESSON 1931 a) and in *Allium schoenoprasum* (TURESSON 1931 b). A tetraploid form of *Vicia cracca* (SWESCHNIKOWA 1928) has, compared to a diploid form, bigger nuclei and cells, broader leaves and a greater number of seeds in the pods. In *Scirpus palustris* HÅKANSSON (1929 b) has observed biotypes with different chromosome numbers. One biotype with 19 chromosome had bigger nuclei and cells and bigger capsules than another biotype with 8 chromosomes. In a similar case in *Callitriche stagnalis* (JØRGENSEN 1925) the biotype with the higher chromosome number had also somewhat bigger fruits. On comparing chromosome number and morphology of plants from Timbuktu (Sahara), HAGERUP (1932) finds that the polyploid species or biotypes are often gigas-types. They also seem to have a greater »vitality» than the diploid relatives.

In several other cases, however, there is no correlation between chromosome number and vegetative vigour. This may be due to the fact that gigantism caused by chromosome increase will be more easily preserved under culture conditions than in nature. It is conceivable that plants of a moderate stature may sometimes be ecologically superior to the giant forms. Therefore, cell number and total size may in nature be reduced by secondary processes, *e. g.* hybridization and subsequent selection. In such cases the influence of the higher chromosome number may be limited to an increase of cell size.

VI.

The primary allo-tetraploid *Galeopsis* plant was called »artificial *Tetrahit*», on account of its conformity in all essential respects with natural *Tetrahit* (cf. MÜNTZING, 1930 b). Now, since a daughter generation from this plant and hybrids with natural *Tetrahit* have been

studied, new facts have been gathered. These facts may be used to decide whether the denominations artificial and synthetic *Tetrahit* are well-grounded or not.

As was expected (1930 b, p. 163), the progeny from the AT-plant (I_1) was not uniform but rather variable. In habitus, however, all the I_1-plants were like natural *Tetrahit*, and also concerning all vegetative characters they were impossible to distinguish from this species. With regard to the network on the middle lap, about two thirds of the plants fulfilled all claims on typical *Tetrahit*-pattern, one third was more or less deviating. Some of those aberrant plants were trisomic, others had the normal chromosome number.

About 40 per cent of the I_1-plants had better pollen fertility than the mother plant. One I_1-plant, which by no means could be morphologically distinguished from pure *Tetrahit*, had even more than 90 per cent good pollen. *Thus, plants have been obtained which genotypically consist of only pubescens- and speciosa-genes but which look like pure Tetrahit, and at the same time are fully fertile.* The high fertility, and the absence or rareness of multivalent formation at the reduction division, make it probable that in subsequent generations constant pure lines will be obtained. As the I_1-plants showed slight morphological differences, the constancy should result not only in one biotype but in an assortment of different lines. The majority of these lines will be undistinguishable from pure *Tetrahit*. The descendants from the aberrant I_1-plants, however, should, if at all constant progenies may be raised from these plants, give rise to biotypes which morphologically must be regarded as *novae species* or perhaps as deviating varieties of *G. Tetrahit*.

A characteristic feature of the primary tetraploid, AT, is that it could not be crossed to the original parents, but without difficulty to natural *Tetrahit* and *bifida*. Neither of the latter species can form hybrids with *pubescens* and *speciosa* (cf. 1930 b, p. 163 ff.). These crossing experiments were repeated with five I_1-plants, chosen at random. These plants all behaved in exactly the same way as the mother plant. In crosses with *Tetrahit* and *bifida* normally developed hybrid seeds were obtained without difficulty in both directions. Crosses with *pubescens* and *speciosa* failed totally, though more than hundred flowers were used for pollination. Therefore, as to crossing possibilities, it is evident that the I_1-plants, and in all probability also the future descendants from these plants, behave in exactly the same way as pure *Tetrahit*.

The significance of this sterility barrier between the allo-tetraploids

and their original parents has been previously discussed (1930 b). The same phenomenon is met with in several other cases of allo- and auto-polyploidy and probably also in many species crosses, when the types crossed have different chromosome number. I have suggested (1930 b, p. 168) that alterations of the normal ratio 2 : 3 : 2 of the chromosome numbers in embryo, endosperm and surrounding somatic tissues is the ultimate cause of embryo abortion or bad seed development, observed in such cases. Then the double fertilization and formation of triploid endosperm may be of considerable significance for the preservation of multiple chromosome numbers among the Angiosperms. — These problems will be further discussed on another occasion.

An *experimentum crucis* with regard to the true nature of the synthetic *Tetrahit*-plants is afforded by the production and study of hybrids between synthetic and pure *Tetrahit*. The study of these hybrids has hitherto given the following main results:

1) The F_1-plants were normally developed and morphologically quite like natural *Tetrahit*.

2) Some of the F_1-hybrids were completely fertile, others partially sterile. In part, this sterility is of the same kind as the intraspecific sterility occurring in natural *Tetrahit*.

3) The chromosome pairing in F_1 was good. One F_1-plant with the normal chromosome number showed 16_{II} at the heterotype metaphase (fig. 83). One trisomic F_1-plant showed either complete pairing (figs. 89—90) or some univalents (fig. 91).

These facts strongly indicate a close genotypic similarity between pure *Tetrahit* and the synthetic types. This similarity is further supported by the fact that both natural and synthetic *Tetrahit* give hybrids with *bifida*, which show a marked decrease in fertility (cf. 1930 a, table 15, p. 241 and table 5 in the present paper).

Thus, to judge from the results hitherto obtained, the majority of the synthetic forms differ essentially from natural *Tetrahit* only in one respect, viz. the constancy. But according to the arguments given above, it is most probably only a question of time that also in this respect similarity to pure *Tetrahit* will be reached. Consequently, the denomination synthetic *Tetrahit* may be regarded as justifiable.

Further it may be stated that the present case essentially represents a clear verification of WINGE's hypothesis (WINGE 1917) that multiple chromosome numbers among wild plant species may result from species hybridization and chromosome doubling. Certainly, a synthesis of an already existing species from two other ones must *a priori* be very difficult,

since other evolutionary processes than chromosome doubling may alter diploids as well as polyploids (cf. WATKINS 1930). Neither do I believe that the natural *Galeopsis Tetrahit* L. has originated in exactly the same way as the synthetic forms. But on basis of my empirical results, I think it logical to state that natural *Tetrahit* in all essentials represents a synthesis of the genes which are now present in *pubescens* and *speciosa*.

Also in a few other cases phylogenetical connections are more or less elucidated by the production of allo-polyploid types.

From the cross *Phleum pratense* (2n) × *P. alpinum* (4n) GREGOR and SANSOME (1930) obtained triploid hybrids and after doubling of the chromosomes four hexaploid plants »of varying fertility» (GREGOR 1931). Other races of *P. pratense* are hexaploid, and therefore the authors suggest that those hexaploids may be the result of natural hybridization of diploid *pratense* with some other plant, in a manner analogous to that described for the artificially produced hexaploid. The natural and artificial hexaploid have been successfully crossed, »giving 161 hybrid plants, many of which are both male- and female-fertile» (GREGOR 1931).

In F_2 of the cross *Salix caprea* × *viminalis* (both diploid) HERIBERT NILSSON (1931) obtained a female plant which morphologically could not be distinguished from *S. cinerea*. This species is tetraploid. The chromosome number of the »*neo-cinerea*»-plant has not yet been determined with certainty, but is evidently higher than in the original parents and »mindestens triploid». From these results HERIBERT NILSSON concludes that natural *Salix cinerea* probably has originated from crosses between *caprea* and *viminalis*. This seems plausible and may be proved by future investigations. In such a case, however, the *neo-cinerea* plant must first be shown to give rise to morphologically similar descendants with the same chromosome number as *cinerea* and which are capable of independent sexual reproduction. The female *neo-cinerea* plant now produced seems to be a parallel to the triploid »pseudo-*Tetrahit*» plant obtained in F_2 of the cross *Galeopsis pubescens* × *speciosa*.

From the same cross, *Salix caprea* × *viminalis*, HERIBERT NILSSON has obtained a hyper-tetraploid (HÅKANSSON 1929 a) F_2-plant which proved to be morphologically identical with the garden »species» *Salix laurina* (HERIBERT NILSSON 1928). *Salix laurina*, however, may only be propagated vegetatively, as it is female and seems to be sterile or almost sterile.

In the genus *Nicotiana* efforts have been made to elucidate the origin and genomatic constitution of some of the tetraploid species, especially *N. tabacum*. On basis of the chromosome pairing observed in various F_1-hybrids and in analogy to the origin of *N. digluta* R. E. CLAUSEN concludes (1928) that »*tabacum* (24_{II}) may have arisen from hybridization of progenitors or close allies of *sylvestris* (12_{II}) and *tomentosa* (12_{II})». BRIEGER (1930) succeeded to obtain a plant, which contained 24 *tabacum*-, 12 *silvestris*- and 12 chromosomes from *Nicotiana Rusbyi*, a species closely related to *tomentosa*. This plant formed 24 bivalents, which shows that all *Rusbyi*- and *silvestris*-chromosomes had found homologues among the *tabacum*-chromosomes, since the chromosomes of the two first-mentioned species are not homologous. Genetic analysis, however, has demonstrated that the two genomes of *tabacum* in several respects are different from the *Rusbyi*- and *silvestris*-genomes.

According to HUSKINS (1931 a, 1931 b) *Spartina Townsendii* is an allo-polyploid species, which in certain localities must have arisen spontaneously from crosses between *S. alterniflora* and *S. stricta*. *Spartina Townsendii* is vigorous and fertile and has the somatic chromosome number 126, which is the sum of the parental chromosome numbers 70 and 56.

An analogous case is represented by *Aesculus carnea* which is a garden plant, produced from crosses between *A. Hippocastanum* and *A. Pavia*. *A. carnea* is rather fertile and constant and has the sum of the chromosomes of *Hippocastanum* and *Pavia* (SKOVSTED 1929). On account of size differences the two parental sets of chromosomes could be identified in the allo-tetraploid hybrid.

Finally, *Rosa Wilsonii*, investigated by BLACKBURN and HARRISON already in 1924, is most probably an allo-polyploid species, arisen from the cross *pimpinellifolia* × *tomentosa*. The primary hybrid must have been triploid. *Rosa Wilsonii* is hexaploid, fertile and has a regular reduction division.

Extensive genome-analytical investigations have been undertaken in the genera *Triticum*, *Aegilops* and *Secale* by numerous investigators (cf. WATKINS 1930, GATES 1931, KIHARA 1930). A special purpose of this analysis is to elucidate the constitution of the hexaploid *vulgare*-wheats. Evidently this work is very difficult on account of the great number of different cross-combinations possible, and hitherto quite definite conclusions have not been reached. However, one thing is clear.

The *vulgare*-wheats and other related polyploid forms are allo-polyploids, and species crossing is the cause of their origin.

When discussing the »*neo-cinerea*» case HERIBERT NILSSON points to the fact that both *Salix cinerea* and *Galeopsis Tetrahit* are anthropochoreous for which reason »auch ihr Wert in der natürlichen Auslese fraglich wird» (1931, p. 318). Further, the author compares these polyploid anthropochoreous plants with polyploid mutants of ornamental plants which may survive under culture conditions but not in nature. Therefore, polyploidy seems to be regarded as a phenomenon, characteristic of cultivated and anthropochoreous plants (cf. also HERIBERT NILSSON 1930, p. 141), and therefore of no evolutionary value.

This view is untenable as polyploidy is also very common among plants which by no means may be suspected of being under the influence of man, *e. g.* plants from alpine or arctic regions, desert plants (cf. HAGERUP 1932), etc. Therefore, if we do not assume that polyploidy among anthropochoreous plants is of an essentially different kind from polyploidy occurring among other plants, it may be considered that cases of experimental species synthesis elucidate an important part of the evolution in higher plants, even if the experimental plants happen to be anthropochoreous.

SUMMARY.

1) In *Galeopsis* allo-tetraploid plants have been produced from crosses and back-crosses, involving the diploid species *pubescens* and *speciosa*. The primary allo-tetraploid plant, AT, had the constitution $\frac{p\ s}{p\ r}$ (cf. p. 134). This plant was used for selfing and for crossing with *G. Tetrahit* and *bifida*.

2) In all morphological respects the I_1-generation was variable, which is in accordance with the genotypical constitution of the mother plant. Two thirds of the I_1-plants could not by any morphological criteria be distinguished from *G. Tetrahit*. One third of the plants was more or less deviating with regard to details of flower shape and colour pattern.

3) Pollen fertility in I_1 was variable. Forty per cent of the plants had higher fertility than the mother individual, their percentage of good pollen ranging from 70 to 95.

4) The F_1-plants from crosses between AT and different *Tetrahit*-lines were normally developed and morphologically typical *Tetrahit*. Some

of the F_1-hybrids were completely fertile, others partially sterile. In part, this sterility is of the same kind as the intraspecific sterility occurring in *G. Tetrahit*. Hybrids with *G. bifida* were vigorous and more sterile than the hybrids with *Tetrahit*.

5) Most of the I_1-plants investigated had the normal chromosome number ($2n = 32$), a few plants were trisomic ($2n = 33$). At the reduction division chromosome pairing was good. Generally 16_{II} were formed but sometimes non-conjunction occurred. True quadrivalents were not observed. In a trisomic plant the extra chromosome was usually free but sometimes member of a trivalent.

6) In hybrids between AT and *Tetrahit*, chromosome pairing was also good. One F_1-plant with the normal chromosome number showed 16_{II} at the heterotype metaphase. A trisomic F_1-plant showed either complete pairing or some univalents.

7) Comparisons with other cases of allo-polyploidy with regard to mode of origin, meiosis, fertility, constancy and morphology are made.

8) The primary allo-tetraploid plant, AT, was called »artificial *Tetrahit*» on account of its conformity in all essential respects with natural *Tetrahit*. The new facts obtained confirm the previous conclusions and demonstrate that natural *Tetrahit* essentially represents a synthesis of the genes present in the diploid species *pubescens* and *speciosa*.

The majority of the synthetic *Tetrahit*-types differ essentially from natural *Tetrahit* only in one respect, viz. the constancy. Most probably it is only a question of time that also in this respect similarity to pure *Tetrahit* will be attained.

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NEUE FÄLLE VON CHROMOSOMENVERKETTUNG IN PISUM

VON *ARTUR HÅKANSSON*
LUND

ES wurde früher über das Vorkommen eines Amphibivalents als eine Kette oder einen Ring aus vier Chromosomen in der Metaphase der ersten Reifeteilung bei *Pisum* ausführlich berichtet (HÅKANSSON 1931). Zusammen sind drei Fälle einer solchen Chromosomenverkettung bekannt: in den Kreuzungen mit der K-Linie von HAMMARLUND, in F_1 Extra Rapid × Soloärt (HÅKANSSON 1929, 1931) und in halbsterilen Pflanzen einer Linie aus Thibet, die PELLEW in Kultur hatte (RICHARDSON 1929). Überall zeichneten sich die Pflanzen mit Verkettung durch eine ungefähr 50 % Gonensterilität aus, in den Kreuzungen mit der K-Linie waren ausserdem gewisse genetische Komplikationen vorhanden, nämlich betreffs Genen, die offenbar in den Chromosomen, die das Amphibivalent bildeten, lokalisiert sind. Ich will hier in aller Kürze über drei neue Fälle von Chromosomenverkettung berichten, weil das zytologische Bild von dem früher beschriebenen teilweise verschieden ist.

Herr ERNST NILSSON, Eslöv, der seit lange die Genetik der Erbse studierte, teilte mir mit, dass in seinen Kulturen mehrere Fälle von Sterilität vorhanden waren. Einige waren in Kreuzungen mit der Sorte Extra Rapid, diese habe ich nicht untersucht, es schien mir nämlich ziemlich sicher, dass Chromosomenringe gefunden werden sollten. Drei der Fälle waren aber nicht durch Extra Rapid hervorgerufen, und über ihre Zytologie kann ich hier berichten. Sie werden im Folgenden N. I, N. II und N. III bezeichnet; die drei Fälle haben ganz verschiedene Abstammung.

In den beiden früher untersuchten Sterilitätsfällen, also Kreuzungen mit der K-Linie und mit Extra Rapid, war das Amphibivalent sehr ähnlich: es war, wie es schien, immer in den Pollenmutterzellen vorhanden, hatte Ring- oder Kettenform, und sehr oft waren infolge Ausbildung s. g. interstitiellen Chiasmata (nach der Terminologie von DARLINGTON) zwei Querarme im Amphibivalent zu sehen. Eines der Chromosomen nahm in der Bildung beider Arme teil, die also benachbarte Fugstellen einnahmen. Mehr selten war ein kurzer dritter Arm

ausgebildet. Das Amphibivalent in N. I und N. II zeigte nun ein ähnliches Verhältnis. In N. II war es als einfache Kette oder Ring ausgebildet und kam in allen Pollenmutterzellen vor, eine kleine Verschiedenheit gab es jedoch: es konnte höchstens ein Querarm beobach-

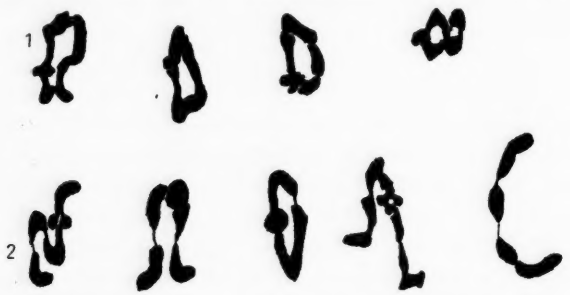

Fig. 1. Amphibivalente von N. I. — Fig. 2. Amphibivalente von N. II. × 2000.

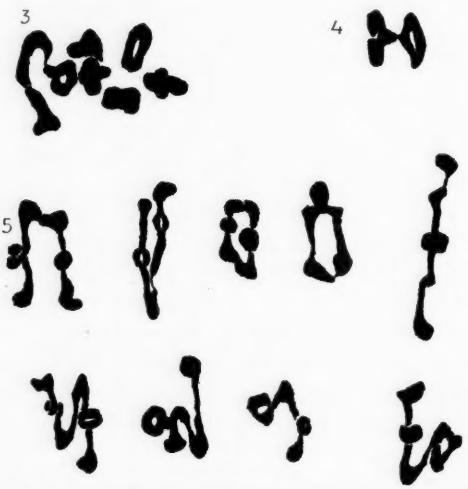

Fig. 3. Metakinese der ersten Reifeteilung von N. III. — Fig. 4. Amphibivalent (?) von N. III. — Fig. 5. Amphibivalente von N. III. × 2000.

tet werden (Fig. 2). Das untersuchte Material ist leider nicht gross, in zwei Präparaten mit zahlreichen, sehr deutlichen Teilungen kamen aber nie zwei Arme im Amphibivalent vor. Die Chromosomen werden offenbar in der Anaphase in verschiedener Weise auf die Pole der Kernspindel verteilt (Fig. 2). Die Chromosomenverteilung 6 + 8 geschieht

nicht selten. Die Teilungen in N. I waren schlechter fixiert, ein Amphibivalent konnte doch leicht beobachtet werden. Es schien von ähnlichem Aussehen wie in N. II (Fig. 1) zu sein.

Die Bildung der Amphibivalente in N. I und N. II sind offenbar durch die Annahme von Austausch zwischen Nicht-Homologen erklärbar (Fig. 6), in ähnlicher Weise wie es betreffs der Kreuzungen mit der K-Linie ausgeführt wurde (HÅKANSSON 1931). Durch den Austausch wird auch die Sterilität hervorgerufen. Das Vorkommen von nur einem Querarm ist nicht ohne Interesse, denn es ist ein Indizium dafür, dass Ausbildung von interstitiellen Chiasmata längs gewisser Teile eines Chromosomen selten sein kann, längs anderer dagegen häufig (HÅKANSSON 1931, S. 54). An zwei Stellen im Amphibivalent kommen unveränderte Chromosomenenden zusammen, nur an einem scheint aber ein Querarm sich ausbilden zu können (Fig. 6).

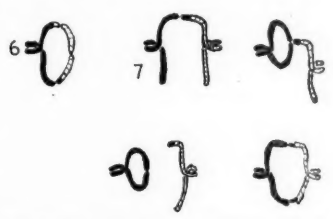

Fig. 6. Schema der Chromosomenbindung in N. II. — Fig. 7. Desgl. N. III.

Das Aussehen des Amphibivalents in N. III ist aber sehr verschieden. Wie in den K-Kreuzungen und in Extra Rapid × Soloärt waren sehr oft zwei Querarme ausgebildet, diese befanden sich aber ausnahmslos an gegenüber einander liegenden Fugstellen (Fig. 5). Nie wurde ein dritter Querarm beobachtet, aber alle Chromosomen können interstitiellen Chiasmata an dem einen Ende bilden. Ein geschlossener Ring kam bisweilen vor, aber viel seltener als in den anderen Sterilitätsfällen. Vielfalls war kein Amphibivalent in der Pollenmutterzelle, es war in zwei Bivalente zerfallen, von denen das eine meist (immer?) offen war. Hierdurch wurde den Eindruck erweckt, dass die Chromosomenverkettung in N. III aus zwei mehr lose gebundenen Bivalenten bestand. Wir finden aber noch eine Eigentümlichkeit, nämlich dass nicht selten drei Chromosomenenden im Amphibivalent vereint sind (»triple chiasma», »Trivalentbindung» [Fig. 3]). Dies wurde in den anderen Fällen von Chromosomenverkettung nicht beobachtet. Dagegen konnte nicht mit Sicherheit entschieden werden, ob bisweilen vier Chromosomenenden vereint sind. Bildungen wie in Fig. 4 sah ich nämlich auch in Pollenmutterzellen, in denen ausserdem ein Amphibivalent war, sie müssten also hier als zufällig verklebten Bivalente gedeutet werden. Eine solche Deutung kann auch dann nicht ausgeschlossen werden, wenn sie die einzige Bivalentenvereinigung in der Zelle ist. Schliess-

lich ist zuzufügen, dass Nichttrennen in der Anaphase selten ist. In 60 Zellen war nur dreimal die Verteilung $6^1/_2 + 7^1/_2$, im übrigen $7 + 7$.

Die Chromosomenverkettung in N. III ist also in mehrfacher Hinsicht von der in den anderen Sterilitätsfällen verschieden. Das Vorkommen von Trivalentbindung macht es wahrscheinlich, dass sie nicht durch Austausch zwischen Nicht-Homologen zu erklären ist. Offenbar sind wenigstens drei identische Chromosomenenden im Amphibivalent. Drei gleiche finden ihre einfachste Erklärung darin, dass eine Translokation von einem Chromosomenende zu dem Ende eines Nicht-Homologen stattgefunden hat. Das fragmentierte Chromosom wäre dann durch ein normales Homologon ersetzt. Ein geschlossener Ring könnte vielleicht durch Crossing-over zwischen Chromatiden entstehen (siehe Fig. 7). Nun muss aber dieser Fall in verschiedener Hinsicht näher untersucht werden, ehe man sich darüber äussern kann, ob eine solche Translokation die Sterilität u. a. erklären kann.

Die erste in *Zea Mays* gefundene Semisterilität wurde anfangs als Translokation erklärt (BRINK und BURNHAM 1929), die Sterilitätsfälle wurden aber nach zytologischen Untersuchungen als Fälle von Austausch zwischen Nicht-Homologen erwiesen (BURNHAM 1930, MCCLINTOCK 1930, COOPER und BRINK 1931). Doch erklärte BURNHAM, dass auch bei einfacher Translokation ein Chromosomenring nach Crossing-over in »four-strand»-Stadium vorkommen könnte. Die in N. III beobachteten Amphibivalente sind aber auch durch Reduplikation eines Chromosomenstückes, so dass vier von den acht Chromosomenenden im Amphibivalent gleich sind, erklärbar (Schema eines solches Falles, siehe DARLINGTON 1931, S. 231).

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HERIBERT NILSSON'S EVIDENCE AGAINST THE ARTIFICIAL PRODUCTION OF MUTATIONS

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IN a recent article in Hereditas (1931), HERIBERT NILSSON argues that the appearance of mutations in increased frequency after treatment with high-energy radiation or high temperature is probably caused by a selective elimination of the normal type, which leaves more mutants to appear, rather than by an actual production of mutations. As evidence for this he presents data which show, firstly, that *Drosophila melanogaster* flies of a »yellow white» stock, when exposed to high temperature while larvae, survived much better than those of a wild-type stock which was treated similarly; secondly, that *Oenothera lamarckiana* seeds aged for several years had greatly reduced viability, but the few which did grow included a very high percentage of so-called »mutants».

It is interesting that larvae of the yellow white stock used should have shown themselves more heat-resistant than those of the morphologically wild-type stock, even though it must be clearly realized that no genetic evidence was presented to show that it was either the gene-difference for yellow versus gray body color or that for white versus red eyes, rather than some other, invisible gene-difference that happened to accompany them, which was responsible for the physiological effect noted. If a separate »physiological» gene-difference existed, a contingency which is not unlikely, it may just as well have been the morphologically wild-type stock which had the mutant allelomorph of this gene, as *vice versa*. In that case it would have been the mutant gene which was selectively eliminated.

However that may be, it is well known that the great majority of mutant types have a lower viability than the normal, most of them, both in the X-ray experiments and in control material, being actually lethal, and that, in general, the more adverse the environmental conditions, including temperature, are, the lower the viability and productivity of the mutants tend to be, relatively to the normals. This is just the opposite of the effect required by HERIBERT NILSSON. While,

however, this rule is a general one, it will be evident that each kind of mutant must have its own specific set of reactions: that one mutant may be actually more resistant to high temperature, another to low temperature, another to drouth, etc., and that one may not legitimately argue from the case of one individual mutant stock to that of another, or from the reactions of a given mutant stock at one stage, or with one agent, to the reactions of the same stock at another stage, or with another agent; still less may one argue from the reactions of just one mutant stock at one stage, with one agent, to the reactions of mutants in general, at any stage, with detrimental agents in general! Yet the sum total of the experience in the *Drosophila* work has been ample to show that, in the great majority of cases, the viability of mutants decreases, relatively to that of normals, with increase in the adversity of environic conditions. Hence the nearest approaches to the ideal Mendelian ratios, crossover frequencies, etc., as observed in counts of the flies that survive to maturity, are usually obtained when culture conditions are optimal.

It is indeed a far cry from the relative viabilities of yellow white versus morphologically wild-type larvae when exposed to heat, to the relative viabilities of all kinds of mutant (mainly lethal) versus normal spermatozoa when exposed to X-rays. It may be recalled that the mutational effect of X-rays on *Drosophila* is especially strong when the irradiation is applied to the spermatozoan stage, as shown in experiments of HARRIS (1929), HANSON (1929 b), and the present author (1930). And yet, as has been shown independently by MOHR (1925) and by MULLER and SETTLES (1927), the genes are actually functionless in the spermatozoa (and also in the haploid stage of the egg). That is, it makes no difference what genes the spermatozoa or eggs themselves contain or lack, their viability and fertilizing capacity is the same regardless of their gametic gene content. The physiological properties of the spermatozoa and eggs depend upon their pre-reductional gene-composition, and upon that of the associated soma. Even if an important section of an autosome is absent or duplicated in the mature gametes, the latter nevertheless have normal viability. Neither X-rays nor other environic conditions, therefore, can exercise the power of selective elimination over the spermatozoa, discriminating between sperm that differ merely with regard to one individual gene. The X-rays certainly damage the sperm, but not selectively, except insofar as the possession of more chromatin might carry with it correspondingly greater possibility of damage. Yet on HERIBERT NILSSON's view, nor-

mal spermatozoa must usually be killed by X-rays far more easily than are spermatozoa carrying genes that are lethal to the zygote!

As evidence of the elimination required on his view, HERIBERT NILSSON calls attention to the high mortality known to occur among *Drosophila* eggs after X-raying (of the spermatozoa). He mentions the fact that the frequency of appearance of mutants may be raised as much as 150 times. This would, on his view, allow not more than about one normal in 150 to develop, *i. e.*, the viability of the fertilized eggs would then be under 0,7 %. Yet the figures on viability of eggs and larvae, published by the present author in the 1928 a article referred to by HERIBERT NILSSON, were, although low, not at all of this order of magnitude. It was stated there (p. 250) that 163 in 569 eggs developed, *i. e.* 1 in $3\,^1/_2$, after a »t2» dose, while the mutation rate, which was 0,1 % in control material, rose to 8,8 % for a »t2» dose, an increase of 88 times. Since the 88-fold increase of mutation rate would on HERIBERT NILSSON's hypothesis require a survival of only one normal egg in 88, it could not possibly be explained in terms of the actually found viability of one egg in $3\,^1/_2$. More detailed work on mortality was later carried out by HANSON (1928), and this too shows clearly a much lesser effect than called for on HERIBERT NILSSON's view. At the lower doses especially, the mortality is rather low, while the mutational effect remains considerable. Our experience has shown that with a dose of about 300 r units the great majority of the fertilized eggs develop, whereas the mutation frequency at this dose is about ten times that of untreated material of the same origin.

HERIBERT NILSSON might, to be sure, maintain that there was an additional mortality of spermatozoa, not fully expressed in the mortality of zygotic stages. But he himself calls attention to the fact that the observed mutation frequency is proportional to the dosage of irradiation used, as has been thoroughly proved by HANSON, HEYS and STANTON (1929, 1930) and by OLIVER (1930, 1932). Now, the mortality is not observed to vary, and would not be expected to vary, according to this rule at all. It follows, and from statistical considerations it would be expected to follow, much more nearly a logarithmic curve, as the dosage is varied. Thus at low dosages of X-ray treatment, viability is decreased only a little when the dosage is doubled, but at high dosages it may be cut to much less than half its previous value when the dosage is doubled; on the other hand the observed mutation frequency preserves throughout an even increase, nicely proportional to

the dosage increase. It is evident therefore that the observed mutation frequency cannot depend upon the mortality.

Although the mutation frequency of *Drosophila* is not raised as much when females are treated as when mature spermatozoa are treated, nevertheless it is raised many fold even by comparatively small doses of irradiation of females, and, on HERIBERT NILSSON's view, this must be accomplished by the killing off of the vast majority of the oögonia, eggs, or larvae that received no lethal or other mutant genes to save their lives. Nevertheless, we do not find anything like a commensurate decrease in the productivity of the rayed females, after small doses of irradiation (300—900 r units). Moreover, when females which are known to be heterozygous for specific mutant genes are X-rayed, there is no adverse effect upon the number of normal versus the number of mutant segregates produced in the next generation. Many such experiments have been reported by MAVOR, and by the present author, and any pronounced effect of this kind could not have escaped notice. This is known to be true even in the case of white eye, as the published records of MAVOR show, although white was the gene which HERIBERT NILSSON regarded as his outstanding example of the effect in question. He would now be reduced to supposing that the catastrophic elimination of normals all occurs in the oögonial stages, and that somehow the few surviving cells quickly replenish the loss of the others. But many of the mutations have been produced by irradiation occurring so shortly before egg-laying that there would be no time for such reduplication. Before reduction, recessives would produce no effect.

As a complete refutation of the mortality hypothesis we may mention the production of mutations in both of two opposite directions, demonstrated by MULLER (1928) and PATTERSON and MULLER (1930) and by TIMOFEËF-RESSOVSKY (1929 a, b, 1930, 1931 a, b). HERIBERT NILSSON himself cites one of the papers of the latter author in which these findings are presented. He does not, however, mention how he reconciles the fact that the frequency of appearance of the mutant »a» from »A» may be increased by the same agent as increases the frequency of appearance of the opposite transformation, namely »A» from »a», if the effect is the result of differential mortality. On the latter view we meet here a hopeless contradiction.

The impossibility of explaining the mutational effect of X-rays by a differential mortality becomes obvious also when we attempt to apply such a principle to the production of mutations in somatic or partially somatic tissue, as in the work of STADLER (1928, 1930), of

PATTERSON (1928, 1929 a, b) and of TIMOFEËF-RESSOVSKY (1929 a, b). In the work of all these investigators gene-mutation frequencies which were many times the spontaneous frequencies were obtained. It would therefore be necessary in all such cases for HERIBERT NILSSON to suppose that the vast majority of cells in the seedling, the embryo, or the larva were killed off, and that nevertheless practically normal development of the plant or the fly, with all organs developing complete, took place from the isolated cells — one in ten or fewer — that remained alive here and there! Moreover, in cases like STADLER's, in which we are not dealing with sex-linked characters in the male, it would be necessary to assume that the *recessive* mutant gene, even though it has been proved to be in heterozygous condition, had the power of saving the life of the cell from the decimating influence of the X-rays. It should be remembered too that this same life-saving gene is usually lethal or semi-lethal to a zygote, when in homozygous condition. These considerations apply also to experiments of the present author, of PATTERSON, and of others on *Drosophila*, in which mutations were produced in diploid cells of females, at stages far removed from that of the mature gamete.

The above arguments have dealt primarily with the evidence regarding the mutational effects of X-rays. It is unfortunate that HERIBERT NILSSON has so indiscriminately lumped together these effects, the effects of moderate differences of temperature, and the effects of excessive heat, for they do not stand upon a common footing. Concerning the lesser effects found by ALTENBURG and the present author, in applying temperature differences within the range that might be termed »normal to the fly», not so much need be said as about the X-ray effects. There is every reason to believe that the higher temperatures used ($27^{\circ} \pm$ C), — at which an approximate doubling of the mutation frequency, in comparison with that at the lower temperatures ($19^{\circ} \pm$ C), was observed, — were not in the slightest degree damaging to the flies or to their germ cells. If they were damaging, then in order to apply HERIBERT NILSSON's principle, it would either have to be assumed, in most of the cases, that the warmth selectively eliminated about twice as many of the normal as of the lethal-bearing gametes — but the reasons why such selection of gametes cannot occur have already been given — or, elimination being supposed to occur in the diploid stage of the cells, the heterozygous recessive lethal gene must again be presumed to save the life of the cell. As in the argument concerning X-rays, this is a virtual *reductio ad absurdum*. We do not

consider it our province here to discuss the evidence concerning the claimed effects of higher degrees of heat, reported positively by GOLDSCHMIDT (1929), by JOLLOS (1930, 1931) and by ROKITSKY (1930), and negatively by FERRY, SHAPIRO and SIDOROFF (1930). Until the inner contradictions in the results with heat, pointed out by ROKITSKY himself, have been cleared up, much must remain questionable concerning the interpretation of the reported positive findings. But, whatever the final interpretation may be, it is clear that it will not be the one offered by HERIBERT NILSSON. For perusal of the foregoing arguments will show that some of the most cogent of them would apply against his interpretation, regardless of the cause of the supposed rise in the general frequency of mutations.

In view of these various strictures, it seems superfluous to consider in detail the reported results concerning the frequency of spurious mutants in late-germinating *Oenothera* seeds. This matter is too remote from that of the production of actual new mutations by X-rays, or even by temperature changes. In fact, insufficient data are provided for the discussion of these results, since data from controls, taken from the same batches of seeds and germinated early, are not given, and it is also not stated whether or not certain particular aberrant types predominate, in the given batches. The phenomenon reported evidently awaits further investigation, but the outcome of the latter will not be able to shake our own results.

In his conclusion, HERIBERT NILSSON seeks to discredit the idea of artificial production of mutations, by calling into question the notion that an important fraction of the natural mutations are produced by natural radiation. The former matter is, however, by no means dependent upon the latter. To clear up the faulty historical impression created by HERIBERT NILSSON's account, it may here be recalled that the latter idea was first suggested by me in 1927, and again in 1928 a and b, as a mere subject *for investigation*, a contingency made possible by the finding of the artificial X-ray mutations, that it was never put forward by me as more than a possibility, and that the necessary investigation was in fact finally carried out and completed by MOTT-SMITH and myself in 1929—30. TIMOFEËF-RESSOVSKY's independent calculations made in the same year (see TIMOFEËF-RESSOVSKY, 1931 b) led to the same conclusions as ours. We found, quite decisively, that the »natural» mutation frequency was far too high to be explained by the natural radiation frequency, and we therefore concluded that the great majority of natural mutations must have some other cause or

causes than radiation. This finding, which is not mentioned by HERIBERT NILSSON although we sent him our reprints, in the title of one of which the result was stated (MULLER and MOTT-SMITH, 1930), is in no way contradictory to the finding that X-rays and radium can be used artificially to produce mutations in abundance. Nor is it antagonistic to the finding that the artificial mutations, though induced by a different primary agent, are in themselves of the same nature as the natural ones, and that they may therefore be used legitimately even in the study of the mechanism of natural mutation, and of gene structure.

In the opinion of the present author, it is not to the advantage of genetics or geneticists for them to be blinded to the existence of any useful method of research. And an unfortunate diversion of time and energy is required when hardwon conclusions are assailed by means of ill-considered evidence, proceeding from sources regarded as authoritative.

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BEITRÄGE ZUR GENETIK VON PHASEOLUS VULGARIS

ZUR VERERBUNG DER TESTAFARBE

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ÜBER die Vererbung der Samenschalenfarbe bei *Phaseolus vulgaris* sind bisher etwa 35 Arbeiten erschienen. Trotz dieser nicht geringen Anzahl von Veröffentlichungen muss gesagt werden, dass auf diesem Gebiete noch grosse Unklarheit herrscht. Eine Zusammenfassung der Ergebnisse dieser Arbeiten in monographischer Form, wobei natürlich zu fordern wäre, dass sich die verschiedenen Einzelresultate gegenseitig ergänzen und zu einem Ganzen zusammengefügt werden können, dürfte gegenwärtig als undurchführbar zu bezeichnen sein. Als Ursachen der hier bestehenden Unklarheit sind hauptsächlich zwei hervorzuheben.

Erstens fehlen in der Mehrzahl der Arbeiten hinlänglich genaue Angaben über die in Rede stehenden Farben, um darüber ins Klare kommen zu können, auf welche Farben die Verfasser abgezielt haben. Dies ist u. a. schon von KRISTOFFERSON (1924) hervorgehoben worden. Die grosse Mehrzahl der Verfasser hat nämlich bei der Beurteilung der Testafarbe kein Standardwerk über Farben (mit Farbenkarten) verwendet. Die verschiedenen Farben wurden ganz einfach mit den in der Umgangssprache gebräuchlichen Ausdrücken »braun», »gelbbraun», »gelb» u. s. w. bezeichnet. Dass diese Bezeichnungsweise ganz ungenügend sein muss, sollte den betreffenden Verfassern eigentlich schon von Beginn an klar gewesen sein, denn man braucht ja nur eine Reihe von Sorten mit verschiedenen Nuancen von z. B. braun unter gleichen Milieuverhältnissen nebeneinander zu bauen um sich davon überzeugen zu können, dass die einzelnen Nuancen konstant verschieden bleiben, demnach erblich bedingt sein müssen. Wird nun eine dieser Nuancen einfach als »braun», »dunkelbraun» oder ähnlich bezeichnet, so ist es für spätere Forscher unmöglich eine sichere Auffassung von der betreffenden Farbe zu erhalten. Es erscheint also in bezug auf die Farben unerlässlich, dieselben auf bestimmte Felder von Farbentafeln zu beziehen, die eventuelle Variation von Nuancen — bedingt durch ver-

schieden gutes Ausreifen, Altern u. dgl. — anzugeben und schliesslich ist es angezeigt die Farben mit den Fachausdrücken zu bezeichnen, wie sie z. B. im Répertoire de Couleurs der Société française des Chrysanthémistes et RENÉ OBERTHUR für 365 Farbentöne (in je 4 Stärkeabstufungen) in fünf Sprachen angegeben sind.

Die zweite und vielleicht schwerwiegendere Ursache der hier herrschenden Unklarheit ist der sozusagen totale Mangel eines Zusammenhanges in genotypischer Hinsicht zwischen den einzelnen Arbeiten. Es ist praktisch genommen gar nie vorgekommen dass ein Forscher die schon früher in anderen Arbeiten behandelten Biotypen sich beschafft hat und seine Untersuchungen dann ausgehend von diesen fortgesetzt hätte. Dies wäre mit Hinsicht auf die komplizierten Verhältnisse bei der Vererbung der Testafarbe von *Phaseolus vulgaris* zur Erzielung von Fortschritten unerlässlich gewesen. So wie es sich gegenwärtig verhält, erscheinen die Ergebnisse der verschiedenen Forscher als isolierte Bruchstücke, die zueinander nicht in sichere Beziehung gebracht werden können. Wir haben hierbei einer Frage von grundlegender Bedeutung zu gedenken, von deren Klarlegung es letzten Endes abhängen wird, ob wir die bisherigen bzw. weitere Resultate zu einem Ganzen vereinigen können werden; es ist dies die Frage nach dem oder den Grundfaktoren für die Ausbildung der Testafarbe und nach dem Verhalten der einzelnen Farbenfaktoren zu diesen.

Die bisher erschienenen Arbeiten geben hierüber — soweit ich habe finden können — keinerlei Aufschlüsse. Sie besprechen stets nur Kreuzungen, in denen eine Spaltung nach meistens einem oder zwei Faktoren stattgefunden hat. Dass bei Abwesenheit eines gewissen Faktors — des Grundfaktors für die Testafarbe — die Samenschale farblos, d. h. weiss ist, ist von mehreren Forschern festgestellt worden. Eine *Bohnenlinie nur mit dem Grundfaktor* für Testafarbe, die, wie ich unten zeigen werde, gleichfalls weisse Samenschale aufweist, scheint indessen bisher kein Forscher in der Hand gehabt zu haben. Unter dieser Voraussetzung also, dass es weisse Bohnen mit und ohne Grundfaktor gibt, von denen die letzteren eine beliebige Anzahl Farbenfaktoren enthalten können, sollen in Kreuzungen von zwei Bohnenlinien mit weissen Samen Nachkommen mit farbigen Samen, und in Kreuzungen von zwei Bohnenlinien mit farbigen Samen Nachkommen mit weissen Samen ausspalten können. Ein Fall wie dieser letztgenannte soll unten eingehender besprochen werden (siehe Kreuzung Nr. XII).

Auf Grund der im Vorstehenden angedeuteten Unklarheit in den bisher vorliegenden Kreuzungsresultaten in bezug auf die Samenfarbe

von *Phaseolus vulgaris* werde ich hier in der Einleitung davon Abstand nehmen eine Übersicht über die Literatur zu geben. Diese soll anstatt dessen nach Besprechung der Kreuzungen und ihrer Ergebnisse diskutiert werden, wobei nur die wichtigeren Mitteilungen — und soweit sich diese mit den vorliegenden Daten in Einklang bringen lassen — berücksichtigt werden sollen. Eine eingehende Erörterung der bisher vorliegenden Literatur beabsichtige ich in einer späteren zusammenfassenden monographischen Darstellung zu geben.

DIE HIER SPALTENDEN TESTAFARBEN.

Die Beurteilung der Testafarben erfolgte an der Hand von drei verschiedenen Arbeiten, nämlich

1. Répertoire de Couleurs publié par la Société française des Chrysanthémistes et RENÉ OBERTHUR, 1905. (Unten abgekürzt zu RC).

2. KLINCKSIECK et VALETTE, Code des Couleurs, Paris 1908. (Unten abgekürzt zu CC).

3. Farbentafeln nach OSTWALD, bearbeitet von der Deutschen Werkstelle für Farbkunde. Ernst Benary, Erfurt. (Unten abgekürzt zu FT).

Erwähnt soll werden, dass nicht alle Nuancen in allen drei Arbeiten vorkommen. So fehlen z. B. in der Farbentafeln nach OSTWALD die grün enthaltenden Nuancen. Ist ein Farbenton in einer Arbeit gut, in einer anderen weniger gut wiedergegeben, so wird nur die erstere Arbeit zitiert.

Die Beurteilung der Samenschalenfarbe ist stets an neu geernteten, gut ausgereiften Samen vorzunehmen, da sich manche Testafarben schon binnen wenigen Monaten verändern. Es findet nicht nur ein Nachdunkeln sondern auch eine Veränderung der Farbe statt. Gewisse Farben scheinen sich dagegen jahrelang unverändert zu halten. In Fällen wo auch die neu geernteten Samen infolge weniger guten Ausreifens keine ganz sichere Beurteilung ihrer Testafarbe gestatteten, ist die nächste Generation zur Entscheidung herangezogen worden.

Reinweiss (Blanc pur, Pure white), RC 1. Die Samenschale ist farblos, sie erscheint aber infolge der durch Luft unter und in derselben bedingten Lichtbrechungsverhältnisse reinweiss. Reinweisser Hilumrand. Letzteres soll hervorgehoben werden, da es Bohnenlinien gibt, die z. B. schwefelgelben Hilumrand besitzen, im übrigen aber ganz reinweiss sind. Reinweisse Bohnen verändern ihre Farbe nur sehr langsam.

nach mehr als einem Jahr, und nehmen dann einen sehr blass schmutziggelblichen Ton an.

Geschwefeltes Weiss (Blanc soufré, Sulphury white), RC 14/3—4, CC 221—203 C, FT 1 ca — 1 ea. Diese Farbe variiert etwas, und kann Töne bis zu Gelblichweiss (Blanc jaunâtre, Yellowish white), RC 13/3—4, annehmen. Schlecht ausgereifte Samen sind glasiger und zeigen die letztgenannte Farbe, die bisweilen noch stärker schmutziggelblich werden kann. Reinweisser Hilumrand. Geschwefeltes Weiss ist eine sehr konstante Farbe und verändert sich auch bei jahrelangem Aufbewahren nur wenig.

Rohseidengelb (Chair saumoné, Pale Ecru), RC 66/1—4, CC 128 D (—146), FT 3,5 ec. Diese Farbe variiert bei gut ausgereiften Samen nur unbedeutend. Schlecht ausgereifte Samen verändern ihre Farbe jedoch beträchtlich und können leicht mit weniger gut ausgereiften Samen der nächsten Farbe (Schamois) verwechselt werden. Dies ist leicht an Proben von einzelnen Pflanzen festzustellen, in denen sowohl gut wie schlecht ausgereifte Samen vorkommen. Farbe des Hilumrandes Bister RC 328/1—2 bis Lichter Ocker RC 326/4. Die Hilumrandfarbe ist übrigens sehr vom guten Ausreifen abhängig; es kommen zum Teil noch hellere, viel häufiger aber dunklere Töne vor. Rohseidengelb bleibt bei längerem Aufbewahren nicht lange konstant, es dunkelt nach und verändert gleichzeitig seine Farbe so stark, dass es nach einigen Jahren nicht mehr erkannt werden kann. Zuerst geht es vom hellsten Rohseidengelb, RC 66/1, allmählich in das dunkelste, RC 66/4, über, dann verändert sich die Farbe bis Isabellfarbig, RC 309/1, und schliesslich bis Abgestorben Laubgelb, RC 321/3. Entsprechende Übergänge in CC sind: 128 C — 128 D — 103 C — 137 — 132 — 127 und dunkler; in FT: 4 ca — 3,5 ea — 4,5 ea — 4,5 gc — 5 gc — 5 ie — 5,5 ng — 5,5 pi.

Schamois (Chamois, Shamois), RC 325/1—2, CC 171, FT 2,5 gc. Diese Farbe zeigt auch bei gut ausgereiften, neu geernteten Samen eine beträchtliche Variation. Die vorstehend zitierten Nummern von Farbenfeldern entsprechen der am häufigsten vorkommenden Nuance. Aber es kommen auch oft mehr oder weniger stark kanarien- bis zitrongelb gefärbte Samen vor; von diesen entsprechen die am stärksten gefärbten RC 17/2 bis 21/2. Entsprechende Variationen sind CC 153 D — 196, FT 4 gc bis 2 ic. Der Hilumrand ist bister, etwa wie bei rohseidengelben Samen, aber häufig etwas dunkler. Schamois verändert sich beim Aufbewahren sehr schnell, es wird viel dunkler und der oben erwähnte, zuweilen stark kanariengelbe Ton verschwindet vollkommen. Nach einem Jahre entspricht die Farbe in der Regel dem dunkelsten Schamois,

RC 325/4, nach ein bis zwei weiteren Jahren wird sie dunkel Haselnussbraun, RC 324/4 und ist dann nicht mehr zu erkennen. Parallel hiermit wird auch die Farbe des Hilumrandes zunehmend dunkler.

. *Bister* (Bistre), RC 328/1—2, CC 152, mitunter etwas heller, selten etwas dunkler gegen CC 128, FT 4,5 pe — 4,5 re. Neu geerntete, gut ausgereifte Samen zeigen nur geringe Farbenvariation, zuweilen findet man noch ein klein wenig hellere Töne als RC 328/1. Der Hilumrand ist dunkelbister, RC 328/4, CC 78—83, nicht selten ist er noch dunkler, Fahlbraun RC 308/4 bis Kastanienbraun RC 341/1—4. Auch diese Samenfarbe verändert sich nach kurzer Zeit, um allmählich Dunkelbister, RC 328/4, mit Übergängen zu Fahlbraun (Fauve), RC 308/1—3, zu erreichen. Gleichzeitig hiermit wird auch der Hilumrand dunkler.

Münzbronze (Bronze de Médaille, Golden bronze green), RC 298/1, selten 298/2; CC 162 (selten bis 129), FT 4 ge, 3,5 lg, selten 4,5 pl. Diese Farbe ist an neugeernteten Samen recht konstant und einheitlich. Der Hilumrand ist Fahlbraun, RC 308/2—3. Beim Aufbewahren dunkeln die Samen ein wenig nach bis dunkel Münzbronze, RC 298/3; gleichzeitig kann auch die Farbe sich etwas Umbra, RC 301/3 nähern.

Mineralbraun, dunkel (Brun minéral, Mineral brown), RC 339/4, CC 104—105, FT 5,5 pi — 5,5 pl, und etwas dunkler mit Übergängen zu Umbra gebrannt, RC 304/2—3. Die hellsten Samen nähern sich in bezug auf die Farbe etwas Dunkel-Brun de Stil oder Rhamninbraun, RC 297/4, FT 5 ri. Wie aus diesen Angaben hervorgeht, stimmt die Farbe nicht ganz exakt mit Mineralbraun, dunkel, überein, sie kommt ihr aber unter den erwähnten Farben am nächsten, weshalb diese Bezeichnung gewählt worden ist. Die Variation dieser Farbe ist im allgemeinen gering. Der Hilumrand ist dunkel Umbra gebrannt, RC 304/4 und noch dunkler bis dunkles Karrobenbraun, RC 342/4. Mineralbraun verändert sich beim Aufbewahren nur wenig, es wird allmählich etwas dunkler.

Kastanienbraun (Marron, Maroon), RC 341/2—4, und bisweilen dunkler mit Übergängen zu dunkel Schwarzviolett, RC 193/4, CC 35—40 —64, TF 7,5 pn — 8,5 pn und dunkler. Diese letzte Farbe (RC 193/4) scheint aber nur sehr selten erreicht zu werden. Nicht gut ausgereifte Samen weichen in der Farbe oft bedeutend ab, indem der grösste Teil der Samenschale dunkel Mineralbraun erscheint. In solchen Fällen tritt aber die richtige Farbe (Kastanienbraun) gewöhnlich recht deutlich in der Nähe des Hilums, häufig über der Radicula und gegenüber dieser zutage, was ein Identifizieren erleichtert. Man bekommt hier den bestimmten Eindruck, dass in der Samenschale zuerst Mineralbraun aus-

gebildet wird und dieses dann durch einen von der Umgebung des Hilums aus fortschreitenden Prozess in Kastanienbraun umgewandelt wird. Der Hilumrand hat hier etwa gleich oder etwas hellere Farbe als die übrige Samenschale. Kastanienbraun zeigt bei längerem Verwahren kaum irgendwelche Veränderungen.

Veilchenviolett, dunkel (Violet de Violette, Violet purple), RC 192/4, aber fast stets dunkler; CC 529—530 (ev. —504), FT 11,5 pl und dunkler. Diese Farbe variiert an gut ausgereiften Samen nur wenig. Der Hilumrand zeigt eine mit der Samenschale übereinstimmende Farbe. Schlecht ausgereifte Samen zeigen so grosse Unterschiede in der Farbe, dass sie ohne besondere Kenntnis der Verhältnisse in der Regel nicht zu erkennen sind. Sie erscheinen schmutzig Schamois, mit mehr oder weniger deutlichem hellviolettem Anflug, der um das Hilum herum am deutlichsten ist. Diese hellviolette Farbe breitet sich dann allmählich über die ganze Testa aus, wobei sie zuerst über der Radicula und um das Hilum ihre endgültige Nuance, dunkel Veilchenviolett, annimmt. Auch hier erhält man den bestimmten Eindruck, dass in der Samenschale zuerst Schamois ausgebildet wird und dieses dann durch einen von der Umgebung des Hilums aus fortschreitenden Prozess in dunkel Veilchenviolett umgewandelt wird. Von der Richtigkeit dieser Verhältnisse habe ich mich durch wiederholtes Aussäen verschiedener solcher Übergangstypen (in F_3, F_4 und F_5) überzeugen können.

Chromgrün (Vert de Chrome, Dark dull green), RC 236/2—4 und noch dunkler. Samen mit dieser Farbe, die — soweit ich hier habe konstatieren können — nur bei einer gewissen Heterozygotie aufgetreten sind, machen in der Regel den Eindruck von fast schwarzen Samen mit einem bläulich-grünen Metallglanz. CC 380 bis Schwarz. In FT kommt diese Farbe nicht vor. Der Hilumrand zeigt gleiche Farbe wie die übrige Samenschale. Diese Farbe scheint sich beim Aufbewahren nicht zu verändern. Wie wir unten sehen werden ist diese Farbe mitunter schwer von schwarz zu unterscheiden.

Schwarz, reines (Noir pur, Black pure), RC 349/4. Samen mit dieser Farbe sind im gut ausgereiften Zustand immer glänzend. Zuweilen kommen Samen mit Elfenbeiner Schwarz (Noir d'Ivoire, Ivory black) RC 350/1—2, vor. Diese Farbe scheint auf unvollkommene Ausfärbung beim Reifeprozess zurückzuführen zu sein. Die von mir gefundenen Spaltungsverhältnisse scheinen wenigstens darzutun, dass diese Farbe nicht an eine bestimmte genetische Konstitution für Schwarz gebunden ist.

Die Farbe des *Hilumrandes* ist im vorliegenden Material immer in

bestimmter Beziehung zur Testafarbe gestanden. Ausnahmen hiervon sind nicht vorgekommen, d. h. jede der oben beschriebenen Testafarben ist stets mit der bei ihr beschriebenen Hilumrandfarbe zusammen aufgetreten. Ein weisser Hilumrand ist also z. B. nur bei den Testafarben Weiss und Geschwefeltes Weiss beobachtet worden. Damit soll nicht gesagt sein, dass dies etwa allgemeine Gültigkeit besitzt; im Gegenteil sind mir verschiedene Fälle bekannt, wo z. B. weisse Testafarbe zusammen mit zitronengelbem oder bister gefärbtem Hilumrand vorkommt, auch Fälle von chromgrünen Samen mit weissem Hilumrand sind mir bekannt. Dies jedoch nur nebenbei.

Fast alle der unten in Kreuzung Nr. II, IV und CIII besprochenen Samentypen zeigten aussen um den Hilumrand noch einen weiteren farbigen Ring, den ich als *Corona* bezeichnen will. Diese Corona ist an der Stelle der Caruncula (Nabelwarze, Strophiola) immer unterbrochen, an der Stelle der Mikropyle ist sie entweder dünner oder unterbrochen. Ist die Corona hier nicht unterbrochen, so macht sie an dieser Stelle eine Ausbuchtung um die Mikropyle herum. Die Farbe der Corona ist gewöhnlich — hier immer — dunkel Grünlichblau, CC 404, bis Chromgrün, etwa RC 236/2. Ob in den unten behandelten Kreuzungen Nr. II, IV und CIII eine Spaltung in bezug auf die Corona vorkommt ist nicht näher untersucht worden. Wahrscheinlich ist dies nicht der Fall, da jedenfalls nur sehr wenige Typen ohne deutliche Corona angetroffen worden sind.

Die Nabelwarze (Caruncula, Strophiola) ist bei allen hier in Frage stehenden Samen mit weissem Hilumrand gleichfalls weiss, bei Samen mit gefärbtem Hilumrand zeigt dieselbe eine stets bedeutend dunklere, aber im übrigen ähnliche Farbe wie dieser. Bei Veilchenviolett, Chromgrün und Schwarz ist die Nabelwarze gleichwie der Hilumrand schwarz. Ausnahmen in bezug auf die Farbe der Nabelwarze von eben Erwähntem sind nicht vorgekommen und mir auch im übrigen nur in ganz vereinzelten Fällen bekannt.

Die Mikropyle hat ähnliche Farbe wie die Umgebung gezeigt.

DIE BENUTZTEN FAKTORENBEZEICHNUNGEN.

Bevor ich an die Besprechung der Kreuzungsresultate schreite, erscheint es mir angebracht kurz die hier verwendeten Faktorenbezeichnungen zu erörtern. Dabei lässt es sich allerdings nicht umgehen schon jetzt im vorweg die wichtigsten Ergebnisse der unten behandelten Kreuzungen anzudeuten. In den meisten Fällen musste die Wahl der Fak-

torenbezeichnungen eine recht willkürliche werden, denn teils konnte oft nicht festgestellt werden auf welche Farbe ein Faktor bezogen worden ist, teils ist ein und dasselbe Symbol für mehrere verschiedene Farben verwendet worden, teils wiederum sind verschiedene Symbole für ein und dieselbe Farbe zur Verwendung gelangt und schliesslich dürfte es sicher sein, dass ein Faktor häufig als allein eine Farbe verursachend angegeben worden ist wo es sich in Wirklichkeit aber um mehrere gehandelt hat.

Von einer Reihe von Forschern ist nachgewiesen worden, dass für die Ausbildung von Pigment in der Samenschale von *Phaseolus vulgaris* die Anwesenheit eines Grundfaktors erforderlich ist. Sämtliche Bohnenbiotypen ohne diesen Grundfaktor — wieviele andere Farbenfaktoren sie auch besitzen mögen — haben weisse (farblose) Testa. Als Symbol für diesen Grundfaktor benutze ich den zuerst von SHULL (1907 b, S. 829) hierfür verwendeten Buchstaben *P*. Später ist von anderen Forschern teils diese Bezeichnung (EMERSON 1909, SHAW and NORTON 1918, SAX und MCPHEE 1923, KRISTOFFERSON 1924, MACHLEJD 1926), teils der Buchstabe *A* hierfür verwendet worden (TSCHERMAK 1912, KOOIMAN 1920, SIRKS 1920, 1922, TJEBBES und KOOIMAN 1922). Der Grundfaktor *P* allein, ohne weitere Farbenfaktoren, verursacht, wie unten in Kreuzung Nr. XII zum erstenmal nachgewiesen wird, keine Farbe. Bohnen mit dem Grundfaktor für Testafarbe allein sind weiss.

Für Geschwefeltes Weiss nehme ich einen Farbenfaktor *C* an, der zusammen mit *P* diese Farbe bedingt. Dieser Faktor verursacht keine Färbung des Hilumrandes. Bohnen mit *C* in heterozygotischer Dosis sind marmoriert — *PPCc* ist demnach marmoriert: Geschwefeltes Weiss auf weissem Grunde. Der Buchstabe *C* ist bisher schon für eine ganze Reihe von verschiedenen Farben verwendet worden, so z. B. von TSCHERMAK (1912) für »Gelbbraun», von SHAW and NORTON (1918) für »Gelb», von LUNDBERG und ÅKERMAN (1917) für »Schokoladen». Bei einem Vergleich der Resultate meiner Kreuzung Nr. XII mit den von den oben zitierten Verfassern mitgeteilten Spaltungsergebnissen wird klar, dass ihr Faktor *C* stets der Ausdruck für mehr als einen einzigen Faktor gewesen ist.

Für Rohseidengelb nehme ich einen Farbenfaktor *J* an, der zusammen mit *P* die Ausbildung dieser Farbe verursacht. Dieser Faktor bedingt gleichzeitig die auf Seite 172 unter »Rohseidengelb» erwähnte Färbung des Hilumrandes. Das Symbol *J* ist — soweit ich finden kann — bisher für Bohnen nicht benutzt worden.

Bei Anwesenheit von sowohl Faktor *C* wie *J* und *P* wird die Samen-

schale Schamois. Ist *C* in heterozygotischer Dosis vorhanden (*PP Cc JJ*) erhalten wir Schamois-marmoriert auf rohseidengelbem Grunde.

Der Effekt der drei weiteren in Rede stehenden Faktoren *G*, *B* und *V* allein in Verbindung mit dem Grundfaktor *P* oder in verschiedenen Verbindungen mit diesem und einem der beiden Faktoren *C* und *J* geht aus den unten zu besprechenden Kreuzungen nicht hervor. Dagegen bringen diese volle Klarheit in bezug auf den Effekt jeder Kombination dieser drei Faktoren auf die Konstitution *PP CC JJ*, d. h. hinsichtlich des Verhaltens dieser drei Faktoren zur Schamois-gefärbten Samenschale.

Der Faktor *G* bedingt eine Veränderung von Schamois zu Bister. Der Buchstabe *G* ist bisher für verschiedene Farben verwendet worden, so z. B. von LUNDBERG und ÅKERMAN (1917) für »Gelbbraun» (= Bister), von SHAW and NORTON (1918) für Schwarz, von SIRKS (1920) für »Gelbbraun», von KRISTOFFERSON (1924) für Schwarz.

Der Faktor *B* verändert Schamois zu Münzbronze. Auch dieser Buchstabe ist bereits in verschiedener Bedeutung verwendet worden. Bei SHULL (1907 b) bedeutet er »Dunkelpurpur», bei EMERSON (1909) »Schwarz», bei TSCHERMAK (1912) »Violett», bei KOOIMAN (1920) »Zitrongelb», u. s. w. JOHANNSEN (1926, S. 443) hat ihn für »Bronze» benutzt.

Den Faktor schliesslich, der Schamois in dunkel Veilchenviolett umwandelt, bezeichne ich mit *V*. Das gleiche Symbol ist von JOHANNSEN (1926, S. 443) für »Violett» benutzt worden.

Ich gebe nun eine Übersicht über alle hier in Rede stehenden Faktorenkombinationen und die durch dieselben bedingten Testafarben. Erwähnt soll werden, dass die meisten Heterozygoten (abgesehen von den Marmorierten) in der Farbe mit dem Auge nicht von den Homozygoten unterschieden werden konnten. Eine einzige Ausnahme bildete das glänzende Chromgrün-Schwarz, dem eine bestimmte heterozygotische Konstitution zukommt. Die beiden hier erschienenen marmorierten Typen gehen mit Heterozygotie des Faktors *C* einher. Folgende Faktorenkombinationen wurden untersucht:

PP cc jj gg bb vv	Weiss
PP Cc jj gg bb vv	Marmoriert Geschwefeltes Weiss/Weiss
PP CC jj gg bb vv	Geschwefeltes Weiss
PP cc JJ gg bb vv	Rohseidengelb
PP cc Jj gg bb vv	
PP Cc Jj gg bb vv	Marmoriert Schamois/Rohseidengelb
PP Cc JJ gg bb vv	

PP CC Jj gg bb vv	Schamois
PP CC JJ gg bb vv	
PP CC JJ Gg bb vv	Bister
PP CC JJ GG bb vv	
PP CC JJ gg Bb vv	Münzbronze
PP CC JJ gg BB vv	
PP CC JJ gg bb Vv	Veilchenviolett, dunkel
PP CC JJ gg bb VV	
PP CC JJ Gg Bb vv	
PP CC JJ Gg BB vv	Mineralbraun, dunkel
PP CC JJ GG Bb vv	
PP CC JJ GG BB vv	
PP CC JJ Gg bb Vv	
PP CC JJ Gg bb VV	Kastanienbraun
PP CC JJ GG bb Vv	
PP CC JJ GG bb VV	
PP CC JJ gg Bb Vv	Chromgrün—Schwarz, glänzend
PP CC JJ gg Bb VV	
PP CC JJ gg BB Vv	
PP CC JJ gg BB VV	
PP CC JJ Gg Bb Vv	
PP CC JJ Gg Bb VV	
PP CC JJ Gg BB Vv	Schwarz
PP CC JJ Gg BB VV	
PP CC JJ GG Bb Vv	
PP CC JJ GG Bb VV	
PP CC JJ GG BB Vv	
PP CC JJ GG BB VV	

KREUZUNG NR. II. TESTAFARBE BISTER × SCHWARZ.

Als Eltern zu dieser Kreuzung wurden benutzt eine »Braune Bohne» von der Firma W. WEIBULL in Landskrona, Stella 0840, eine reine Linie (L. 1) mit der Testafarbe *Bister*, sowie ein einheitlicher Stamm der bekannten Wachsbohne Neger (0850) mit rein *schwarzen* Samen. Die Samenschalen beider Eltern sind glänzend. Beide sind typische niedrige Bohnen. Die Blütenfarbe von Stella ist Laeliafarbig, blass, ähnlich RC 187/1, aber viel blasser, die von Neger ist Bischofsviolett, hell, RC 189/1, jedoch etwas lebhafter. Die Hülsenfarbe von Stella ist mittelgrün, die von Neger das für Wachsbohnen charakteristi-

sche Gelb. Diese Eigenschaften seien nur nebenbei erwähnt, da ihre Vererbung in vorliegender Arbeit nicht behandelt werden soll.

Die Kreuzungen wurden 1926 in beiden Richtungen ausgeführt. Es wurden etwa 30 F_1-Samen erhalten. Die F_1-Generation dieser Kreuzung gelangte in einem für den Bohnensamenbau ausserordentlich ungünstigen Jahre, 1927, zur Entwicklung. Ein beträchtlicher Teil der erhaltenen Samen war schlecht ausgereift, was zur Folge hatte, dass in der zweiten Generation im Jahre 1928 nur 174 Pflanzen erhalten wurden. Die Samen dieser Generation waren sehr gut ausgebildet.

An F_1 wurde folgendes beobachtet. Es dominierte die Blütenfarbe von Neger, Bischofsviolett, anscheinend vollkommen über die von Stella, blass Laeliafarbig. Es dominierte die Hülsenfarbe von Stella, Grün, anscheinend vollkommen über die gelbe Hülsenfarbe von Neger. Die auf F_1 erhaltenen Samen (F_2-Samen) hatten glänzend rein schwarze Testafarbe, gleichwie die von Neger. Die Samenformen der beiden Eltern weichen nur ganz unbedeutend voneinander ab, die Form der F_2-Samen stimmt mit diesen überein. Hier eventuell vorhandene Abweichungen könnten nur durch ganz genaue Messungen festgestellt werden.

Die auf F_2 erhaltenen Samen zeigten mit Hinsicht auf die Testafarbe die in Tabelle 1 mitgeteilten Spaltungsresultate. Die gefundenen Zahlen stimmen ziemlich gut mit folgendem theoretischen Verhältnis: 36 Schwarz : 9 Kastanienbraun : 9 Mineralbraun : 3 Veilchenviolett : 3 Münzbronze : 3 Bister : 1 Schamois. Wir haben es also allem Anschein nach mit einer trifaktoriellen Spaltung zu tun. Werden die erhaltenen Spaltungszahlen auf die Kombinationszahl 64 umgerechnet, resultiert an Stelle des oben angeführten theoretischen Verhältnisses das folgende: $34{,}_{94} : 11{,}_{40} : 8{,}_{09} : 2{,}_{21} : 2{,}_{58} : 2{,}_{94} : 1{,}_{84}$. Die für D/m berechneten Werte (siehe Tab. 1) zeigen an, dass die erhaltenen Zahlen für dieses Spaltungsverhältnis statistisch sicher sind. Volle Klarheit in bezug auf die genotypische Konstitution der hier spaltenden Typen kann natürlich erst in einer folgenden Generation gewonnen werden.

Unter Hinweis auf die Auseinandersetzung im vorigen Abschnitt über Faktorenbezeichnung bezeichne ich die drei hier an der Spaltung beteiligten Faktoren mit *G*, *B* und *V*. Sämtliche hier in Rede stehenden Typen müssen überdies noch wenigstens drei andere Faktoren für Testafarbe besitzen. Nämlich erstens den Grundfaktor für die Ausbildung von Farbe *P* und zweitens die beiden Faktoren *C* und *J*, die zusammen die Farbe Schamois bedingen. Der Beweis für die letztere Behauptung soll später bei der Besprechung von Kreuzung Nr. XII erbracht werden.

TABELLE 1. *F_2 der Kreuzung II: L. 1, Bister × 0850, Schwarz.*
(D/m berechnet für das theoretische Spaltungsverhältnis 36 : 9 : 9 : 3 : 3 : 3 : 1.)

Nr.	Schwarz	Kastanienbraun	Mineralbraun (dunkel)	Veilchenviolett (dunkel)	Münzbronze	Bister	Schamois	Summe
15110	19	3	6	1	—	—	1	30
D/m	0,78	0,62	1,12	0,34	1,21	1,21	0,45	—
15111	30	7	5	1	6	—	3	52
D/m	0,21	0,12	0,92	0,94	2,32	1,60	2,46	—
15112	18	4	4	2	1	2	—	31
D/m	0,20	0,19	0,19	0,47	0,38	0,47	0,70	—
15113	13	9	3	2	1	4	—	32
D/m	1,78	2,28	0,76	0,42	0,42	2,08	0,71	—
15114	14	10	4	—	—	—	1	29
D/m	0,87	3,16	0,04	1,19	1,19	1,19	0,68	—
Summen:	94	33	22	6	8	6	5	174
Erwartet:	97,85	24,46	24,46	8,16	8,16	8,16	2,72	—
D/m	0,59	1,86	0,54	0,77	0,06	0,77	1,52	—

TABELLE 2. *Spaltung von Schwarz: PP CC JJ Gg Bb Vv in F_3 der Kreuzung II.*

Nr.	Schwarz	Kastanienbraun	Mineralbraun (dunkel)	Veilchenviolett (dunkel)	Münzbronze	Bister	Schamois	Summe
15110/2	7	2	2	1	1	2	—	15
15110/4	8	2	1	2	—	2	—	15
15110/14	3	—	1	—	1	1	—	6
15111/15	4	4	3	—	—	1	—	12
15111/19	9	2	3	1	1	1	—	17
15111/22	5	—	2	—	1	1	—	9
15111/47	6	2	1	2	1	—	—	12
15112/3	8	2	4	—	3	—	—	17
15112/9	18	3	5	1	2	1	2	32
15112/11	15	2	1	—	1	2	—	21
15112/13	11	3	4	2	2	2	—	24
15112/19	10	5	7	1	—	2	1	26
15112/29	10	4	4	2	—	2	—	22
15113/21	13	2	2	1	—	4	—	22
15114/18	15	—	5	2	1	4	1	28
15114/25	11	3	1	1	1	1	—	18
15114/30	16	4	2	1	1	—	—	24
Summen:	169	40	48	17	16	26	4	320
Erwartet:	180	45	45	15	15	15	5	—
D/m für 36 : 9 : : 9 : 3 : 3 : 3 : 1	1,24	0,80	0,48	0,53	0,26	2,91	0,45	—

TABELLE 3. *Spaltung von Schwarz: PP CC JJ GG Bb Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Schwarz	Kastanien-braun	Mineral-braun (dunkel)	Bister	Summe
F_3	15110/3	22	2	7	1	32
»	15110/8	19	3	8	2	32
»	15111/5	1	1	2	—	4
»	15111/8	7	1	2	—	10
»	15111/21	3	1	2	—	6
»	15111/29	7	1	4	1	13
»	15111/43	28	11	15	3	57
»	15111/44	6	2	4	—	12
»	15111/45	10	5	5	2	22
»	15112/18	12	2	2	—	16
»	15112/22	28	8	9	2	47
»	15113/2	10	4	1	—	15
»	15113/7	13	9	3	1	26
»	15113/13	7	4	2	2	15
»	15113/23	4	2	1	1	8
»	15114/4	18	5	6	3	32
F_4	10211	2	1	1	1	5
Summen:	—	197	62	74	19	352
Erwartet:	—	198	66	66	22	—
D/m für 9:3:3:1	—	0,11	0,55	1,09	0,66	—

TABELLE 4. *Spaltung von Chromgrün—Schwarz: PP CC JJ gg Bb Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Schwarz u. (Chrom-grün)	Veilchen-violett (dunkel)	Münz-bronze	Schamois	Summe
F_3	15110/25	27	7	6	1	41
»	15111/2	11	1	5	1	18
»	15111/23	11	5	6	4	26
»	15111/31	16	6	3	1	26
»	15111/32	7	—	2	1	10
»	15111/41	2	1	1	—	4
»	15112/12	11	1	4	—	16
»	15112/16	18	4	10	4	36
»	15112/27	11	—	8	—	19
»	15113/28	12	5	5	3	25
»	15114/27	9	2	2	—	13
»	15114/29	4	1	—	1	6
F_4	10219	8	5	2	2	17
»	10234	12	2	2	2	18
Summen:	—	159	40	56	20	275
Erwartet:	—	154,69	51,56	51,56	17,19	—
D/m für 9:3:3:1	—	0,52	1,78	0,69	0,70	—

TABELLE 5. *Spaltung von Schwarz: PP CC JJ Gg Bb VV in F_2 der Kreuzung II.*

Nr.	Schwarz	Kastanienbraun	Veilchenviolett (dunkel)	Summe
15111/13	14	4	3	21
15111/18	17	10	3	30
15111/20	12	9	1	22
15112/5	8	2	1	11
15112/14	6	4	1	11
Summen:.....	57	29	9	95
Erwartet:	71,25	17,81	5,94	—
D/m für 12 : 3 : 1	3,38	2,93	1,30	—

TABELLE 6. *Spaltung von Schwarz: PP CC JJ Gg BB Vv in F_2 der Kreuzung II.*

Nr.	Schwarz	Mineralbraun (dunkel)	Münzbronze	Summe
15112/1	24	2	3	29
15113/14	13	7	4	24
15114/21	4	1	1	6
15114/28	27	3	1	31
Summen:.....	68	13	9	90
Erwartet:	67,50	16,88	5,62	—
D/m für 12 : 3 : 1	0,12	1,05	1,47	—

TABELLE 7. *Spaltung von Schwarz: PP CC JJ GG Bb VV in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Schwarz	Kastanienbraun	Summe
F_3	15110/1	24	7	31
»	15110/30	3	1	4
»	15112/7	7	8	15
»	15112/24	4	1	5
»	15113/19	7	2	9
»	15114/13	10	5	15
»	15114/17	21	5	26
F_4	10201	20	6	26
»	10202	8	5	13
»	10210	19	2	21
»	10212	8	4	12
Summen:.....	—	131	46	177
Erwartet:	—	132,75	44,25	—
D/m für 3 : 1.....	—	0,30	—	—

TABELLE 8. *Spaltung von Schwarz: PP CC JJ GG BB Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Schwarz	Mineralbraun (dunkel)	Summe
F_3	15110/15	11	3	14
»	15110/18	6	2	8
»	15111/39	10	7	17
»	15111/46	4	3	7
»	15112/21	21	6	27
»	15112/28	7	1	8
»	15113/25	9	4	13
»	15114/24	3	2	5
F_4	10217	17	2	19
»	10228	18	5	23
Summen:	—	106	35	141
Erwartet:	—	105,75	35,25	—
D/m für 3:1	—	0,05	—	—

TABELLE 9. *Spaltung von Schwarz: PP CC JJ gg Bb VV in F_3 der Kreuzung II.*

Nr.	Schwarz	Veilchenviolett (dunkel)	Summe
15110/6	11	5	16
15110/7	16	8	24
15110/29	3	3	6
15114/12	8	1	9
15114/15	6	2	8
Summen:	44	19	63
Erwartet:	47,25	15,75	—
D/m für 3:1	0,94	—	—

TABELLE 10. *Spaltung von Schwarz: PP CC JJ gg BB Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Schwarz	Münzbronze	Summe
F_3	15110/22	5	1	6
»	15110/23	8	2	10
»	15111/17	5	2	7
»	15111/26	6	4	10
F_4	10208	17	9	26
»	10218	13	6	19
»	10220	18	6	24
»	10222	14	3	17
Summen:	—	86	33	119
Erwartet:	—	89,25	29,75	—
D/m für 3:1	—	0,69	—	—

TABELLE 11. *Spaltung von Kastanienbraun: PP CC JJ Gg bb Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Kastanienbraun	Veilchenviolett (dunkel)	Bister	Schamois	Summe
F_3	15111/28	4	2	1	2	9
»	15111/34	29	9	8	2	48
»	15111/50	22	2	5	3	32
»	15112/15	22	5	6	3	36
»	15112/31	7	3	4	—	14
»	15113/3	25	7	6	4	42
»	15113/17	1	3	1	2	7
»	15114/3	17	3	3	—	23
»	15114/5	11	2	2	2	17
»	15114/6	15	6	4	—	25
»	15114/7	2	—	—	1	3
»	15114/20	12	5	1	1	19
F_4	10206	4	—	2	1	7
»	10230	15	4	3	2	24
»	10238	12	6	2	1	21
Summen:	—	198	57	48	24	327
Erwartet:	—	183,94	61,31	61,31	20,44	—
D/m für 9 : 3 : 3 : 1	—	1,57	0,61	1,89	0,81	—

TABELLE 12. *Spaltung von Kastanienbraun: PP CC JJ Gg bb VV in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Kastanienbraun	Veilchenviolett (dunkel)	Summe
F_3	15110/19	20	7	27
»	15111/33	19	6	25
»	15112/23	2	1	3
»	15112/26	17	6	23
»	15113/1	8	5	13
»	15114/9	34	12	46
»	15114/31	33	10	43
F_4	10232	15	6	21
»	10233	16	4	20
»	10239	17	5	22
Summen:	—	181	62	243
Erwartet:	—	182,25	60,75	—
D/m für 3 : 1	—	0,19	—	—

TABELLE 13. *Spaltung von Kastanienbraun: PP CC JJ GG bb Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Kastanien-braun	Bister	Summe
F_3	15110/5	17	7	24
»	15111/3	8	3	11
»	15111/25	14	7	21
»	15113/6	19	1	20
»	15113/10	15	6	21
»	15114/22	35	9	44
F_4	10227	13	4	17
Summen:	—	121	37	158
Erwartet:	—	118,50	39,50	—
D/m für 3:1	—	0,37	—	—

TABELLE 14. *Spaltung von Mineralbraun: PP CC JJ Gg Bb vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr	Mineral-braun (dunkel)	Münz-bronze	Bister	Schamois	Summe
F_3	15111/6	9	2	2	1	14
»	15111/42	7	2	1	—	10
»	15112/20	1	2	2	—	5
»	15113/33	3	1	1	—	5
»	15114/23	18	7	4	—	29
»	15114/26	9	—	—	2	11
F_4	10245	10	4	1	1	16
Summen:	—	57	15	14	4	90
Erwartet:	—	50,63	16,87	16,87	5,63	—
D/m für 9:3:3:1	—	1,30	0,77	0,50	0,71	—

TABELLE 15. *Spaltung von Mineralbraun: PP CC JJ Gg BB vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Mineralbraun (dunkel)	Münzbronze	Summe
F_3	15110/27	5	1	6
»	15111/12	6	2	8
»	15111/48	9	3	12
»	15112/4	7	2	9
»	15112/48	25	13	38
»	15114/11	6	2	8
F_4	10241	14	10	24
»	10247	15	2	17
Summen:	—	87	35	122
Erwartet:	—	91,50	30,50	—
D/m für 3:1	—	0,94	—	—

TABELLE 16. *Spaltung von Mineralbraun: PP CC JJ GG Bb vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Mineralbraun (dunkel)	Bister	Summe
F_3	15110/9	5	2	7
»	15110/11	16	10	26
»	15113/15	5	2	7
F_4	10226	13	2	15
»	10246	14	8	22
Summen:	—	53	24	77
Erwartet:	—	57,75	19,25	—
D/m für 3:1	—	1,25	—	—

TABELLE 17. *Spaltung von Veilchenviolett: PP CC JJ gg bb Vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Veilchenviolett (dunkel)	Schamois	Summe
F_3	15111/24	23	5	28
»	15112/32	20	4	24
»	15113/8	7	4	11
F_4	10203	21	3	24
»	10204	17	5	22
»	10235	21	6	27
»	10237	19	5	24
»	10248	12	2	14
»	10249	20	7	27
»	10250	15	8	23
»	10251	15	6	21
»	10270	19	8	27
Summen:	—	209	63	272
Erwartet:	—	204	68	—
D/m für 3:1	—	0,70	—	—

TABELLE 18. *Spaltung von Münzbronze: PP CC JJ gg Bb vv in F_3 der Kreuzung II.*

Nr.	Münzbronze	Schamois	Summe
15111/10	13	4	17
15111/16	10	1	11
15111/36	12	5	17
15111/52	2	2	4
Summen:	37	12	49
Erwartet:	36,75	12,25	—
D/m für 3:1	0,08	—	—

TABELLE 19. *Spaltung von Bister: PP CC JJ Gg bb vv in F_3 und F_4 der Kreuzung II.*

Generation	Nr.	Bister	Schamois	Summe
F_3	15112/10	9	4	13
»	15113/18	18	7	25
F_4	10207	9	2	11
Summen:	—	36	13	49
Erwartet:	—	36,75	12,25	—
D/m für 3 : 1	—	0,25	—	—

Schamois, dem die Formel *PP CC JJ* zukommt (siehe Kreuzung XII), wird durch die Anwesenheit eines weiteren Faktors, *G*, in Bister umgewandelt. Die Testafarbe von Stella wäre demnach durch folgende Formel auszudrücken: *PP CC JJ GG bb vv*. Für die Testafarbe des anderen Elters, Neger, wollen wir einstweilen folgende Konstitution annehmen: *PP CC JJ gg BB VV*. Diese Annahme entspricht insofern den Spaltungsresultaten in F_2 als wir bei dieser Konstitution der beiden Eltern erstens eine trifaktorielle Spaltung bekommen und dass es zweitens zu einer Abspaltung von Schamois gefärbten Bohnen kommt, welcher Farbe die Formel *PP CC JJ gg bb vv* zukommt. Ausserdem ersehen wir aus F_2 dass die Ausbildung der schwarzen Testafarbe im vorliegenden Falle von der An- bzw. Abwesenheit des Faktors *G* unabhängig ist. Hier liegt ein schöner Fall von Epi- bzw. Hypostasie vor. Der Effekt des Faktors *G* wird von der Schwarz bedingenden Konstitution vollkommen gedeckt. Auf diesen Fall soll später zurückgekommen werden.

Eine weitere an den Samen von F_2 gemachte Beobachtung verdient erwähnt zu werden. Unter den 94 Pflanzen mit schwarzen Samen befanden sich, ausser reinschwarzen mit Übergängen zu Elfenbeinschwarz, 11 Pflanzen, bei denen die Samenschale ein glänzendes Chromgrün-Schwarz (grünlichblau glänzend) zeigte. Ein weitere, zwölfte Pflanze war in dieser Hinsicht zweifelhaft und wurde als Schwarz klassifiziert. Ich dachte mir zuerst dass diese Erscheinung auf verschiedenes Ausreifen zurückzuführen sei. Wie wir sehen werden, hat sich dann in der dritten Generation herausgestellt, dass allen diesen 12 Pflanzen eine ganz bestimmte heterozygotische Konstitution zukommt, und zwar *PP CC JJ gg Bb Vv*. In Tabelle 1 (F_2) sind die betr. Pflanzen unter Schwarz angeführt.

Bei Richtigkeit obiger Annahmen soll den F_1-Samen folgende Kon-

stitution in bezug auf die Testafarbe zukommen: *PP CC JJ Gg Bb Vv*. Die Spaltung tritt erst an den F_3-Samen auf, da die Samenschale bei diesen der F_2-Generation angehört. Unter Berücksichtigung nur der drei Faktoren in heterozygotischer Dosis erhalten wir folgendes Spaltungsschema.

F_1	Spaltung in F_2		Spaltung in F_3
	1 *GG BB VV*	Schwarz	Konstant
	2 *Gg BB VV*	»	Konstant
	2 *GG BB Vv*	»	3 Schwarz : 1 Mineralbraun
	4 *Gg BB Vv*	»	12 Schwarz : 3 Mineralbraun : 1 Münzbronze
	4 *Gg Bb VV*	»	12 Schwarz : 3 Kastanienbraun : 1 Veilchenviolett
	4 *GG Bb Vv*	»	9 Schwarz : 3 Kastanienbraun : 3 Mineralbraun : 1 Bister
	8 *Gg Bb Vv*	»	36 Schwarz : 9 Kastanienbraun : 9 Mineralbraun : 3 Veilchenviolett : 3 Münzbronze : 3 Bister : 1 Schamois
Gg Bb Vv	2 *GG Bb VV*	»	3 Schwarz : 1 Kastanienbraun
Schwarz	1 *gg BB VV*	»	Konstant
	2 *gg BB Vv*	»	3 Schwarz : 1 Münzbronze
	2 *gg Bb VV*	»	3 Schwarz : 1 Veilchenviolett
	4 *gg Bb Vv*	Chromgrün-Schw.	9 Schwarz (einschl. Chromgrün-Schwarz): 3 Veilchenviolett : 3 Münzbronze : 1 Schamois
	1 *GG bb VV*	Kastanienbraun	Konstant
	2 *GG bb Vv*	»	3 Kastanienbraun : 1 Bister
	2 *Gg bb VV*	»	3 Kastanienbraun : 1 Veilchenviolett

4	*Gg bb Vv*	Kastanienbraun	9 Kastanienbraun : 3 Veilchenviolett : 3 Bister : 1 Schamois
1	*GG BB vv*	Mineralbraun	Konstant
2	*GG Bb vv*	»	3 Mineralbraun : 1 Bister
2	*Gg BB vv*	»	3 Mineralbraun : 1 Münzbronze
4	*Gg Bb vv*	»	9 Mineralbraun : 3 Münzbronze : 3 Bister : 1 Schamois
1	*gg bb VV*	Veilchenviolett	Konstant
2	*gg bb Vv*	»	3 Veilchenviolett : 1 Schamois
1	*gg BB vv*	Münzbronze	Konstant
2	*gg Bb vv*	»	3 Münzbronze : 1 Schamois
1	*GG bb vv*	Bister	Konstant
2	*Gg bb vv*	»	3 Bister : 1 Schamois
1	*gg bb vv*	Schamois	Konstant

Die in F_3 erhaltenen Spaltungsresultate, die in den Tabellen 2—19 wiedergegeben sind, stimmen durchweg mit den laut obigem Schema zu erwartenden Ergebnissen überein. Die dritte Generation ist während der Jahre 1929 und 1930 aufgezogen worden, 1930 überdies noch eine vierte Generation, deren Resultate ganz mit jenen der dritten übereinstimmen. In der dritten und vierten Generation wurden für die Untersuchung der Vererbung der Testafarbe insgesamt 4186 Individuen aufgezogen. Von diesen waren nach F_2 1167 in bezug auf die Testafarbe konstant geblieben, die übrigen 3019 spalteten.

Laut vorstehendem Schema soll Schwarz — wenn von Chromgrün-Schwarz abgesehen wird — in F_3 in acht verschiedenen Weisen aufspalten. Dies ist auch eingetroffen. Die betreffenden Resultate sind in den Tabellen 2, 3 und 5—10 zu finden. Wie aus diesen ersichtlich ist, geben die Werte für D/m mit Ausnahme der Spaltung in Tab. 5 durchweg statistische Sicherheit an. Ob die Spaltung von Schwarz *PP CC JJ Gg Bb VV* (Tab. 5) wirklich nach dem Verhältnis 12 Schwarz : 3 Kastanienbraun : 1 Veilchenviolett erfolgt oder ob hier auf Grund von (schwacher) Koppelung bzw. einer anderen Komplikation mit einem abweichenden Verhältnis zu rechnen ist, lässt sich an der Hand des geringen hierfür vorliegenden Materials nicht entscheiden. Diese Frage soll zum Gegenstand einer besonderen Untersuchung gemacht werden.

Die Spaltung von Chromgrün-Schwarz in F_3 beweist erst die oben angenommene Konstitution. Diese erscheint nun sicher, da die Nachkommen solcher Samen niemals eine andere Spaltung gezeigt haben. Ausserdem sind keine konstant bleibenden chromgrün-schwarzen Samen erhalten worden. Von den übrigen schwarzsamigen Pflanzen wurden in F_3 325 Individuen mit konstant schwarzen Samen bekommen.

Auch die Aufspaltungen der Testafarben Kastanienbraun, Mineralbraun, Veilchenviolett, Münzbronze und Bister erfolgte in voller Übereinstimmung mit obigem Schema. Die Werte für D/m sind in allen diesen Fällen unter 2,0 gelegen (siehe Tabelle 11—19). Die Anzahl von Pflanzen mit konstanter Testafarbe betrug in F_3 für die verschiedenen Farben: Kastanienbraun 154, Mineralbraun 92, Veilchenviolett 55, Bister 156 und Münzbronze 124. Mit der Farbe Schamois wurden — wie erwartet — nur Pflanzen mit konstant gefärbten Samen (251) erhalten.

KREUZUNG NR. IV. TESTAFARBE BISTER × SCHWARZ.

Als Eltern zu dieser Kreuzung wurden zwei reine Linien benutzt: L. 25, eine reine Linie aus »Braune Bohne» mit Bister Testafarbe sowie L. 24, eine reine Linie aus der in Schweden recht gebräuchlichen Wachsbohne »Merveille du Marché» mit rein schwarzen Samen. Beide Linien sind typisch niedrig. Die Blütenfarbe von L. 25 ist blass Laeliafarbig, die von L. 24 hell Bischofsviolett. Die Hülsenfarbe von L. 25 ist mittelgrün, die von L. 24 gelb wie bei Neger, 0850, in Kreuzung II. Beide Linien haben glänzende Samenschale.

Kreuzungen zwischen diesen beiden Linien wurden in beiden Richtungen im Jahre 1928 und 1929 ausgeführt. Wie aus Obenstehendem hervorgeht, stimmen die Eigenschaften Testafarbe, Blütenfarbe und Hülsenfarbe der zur Kreuzung IV verwendeten Linien mit jenen der Eltern von Kreuzung II überein. In F_1 wurden auch hinsichtlich dieser Eigenschaften ganz gleiche Resultate erhalten wie in Kreuzung II. So dominierte in F_1 die Blütenfarbe Bischofsviolett anscheinend vollkommen über Laeliafarbig, die Hülsenfarbe Grün anscheinend vollkommen über Gelb und die schwarze Testafarbe über Bister. In F_2 wurde in bezug auf die Testafarbe genau die gleiche trifaktorielle Spaltung konstatiert wie in Kreuzung II. Bei einer Umrechnung der Spaltungszahlen auf die Kombinationszahl 64 wurde erhalten: 36,5 Schwarz (einschl. Chromgrün-Schwarz) : 8,40 Kastanienbraun : 9,20 Mineralbraun : 2,60 Veilchenviolett : 2,80 Münzbronze : 3,60 Bister : 0,90 Schamois, was gut mit dem theoretischen Verhältnis 36 : 9 : 9 : 3 : 3 : 3 : 1 übereinstimmt. Die

TABELLE 20. *F_2 der Kreuzung IV: L. 25, Bister × L. 24, Schwarz.*
(D/m berechnet für das theoretische Spaltungsverhältnis 36 : 9 : 9 : 3 : 3 : 3 : 1.)

Nr.	Schwarz	Kastanienbraun	Mineralbraun (dunkel)	Veilchenviolett (dunkel)	Münzbronze	Bister	Schamois	Summe
10331	16	2	5	1	0	2	1	27
D/m	0,30	0,99	0,66	0,24	1,15	0,67	0,91	—
10332	1	0	0	0	1	2	0	4
D/m	1,25	0,81	0,81	0,45	1,93	4,30	0,25	—
10333	25	4	6	1	0	3	1	40
D/m	0,80	0,74	0,17	0,65	1,40	0,85	0,47	—
10334	27	10	8	4	4	3	2	58
D/m	1,49	0,69	0,06	0,80	0,80	0,17	1,14	—
10335	15	0	3	1	0	1	0	20
D/m	1,69	1,81	0,12	0,06	0,99	0,06	0,58	—
10336	15	5	4	1	1	1	0	27
D/m	0,08	0,66	0,11	0,24	0,24	0,24	0,65	—
10337	12	8	5	3	2	3	0	33
D/m	2,30	1,67	0,18	1,20	0,38	1,20	0,73	—
10338	34	4	8	0	3	1	0	50
D/m	1,67	1,23	0,39	1,57	0,44	0,90	0,89	—
10339	30	5	6	2	1	2	0	46
D/m	1,23	0,62	0,19	0,11	0,81	0,11	0,86	—
10340	42	9	9	1	1	6	0	69
D/m	0,77	1,14	1,28	1,27	1,27	1,57	1,05	—
10341	30	7	9	4	3	2	2	57
D/m	0,56	0,38	0,38	0,84	0,20	0,42	1,20	—
10342	12	3	4	0	1	0	0	20
D/m	0,34	0,12	0,77	0,99	0,06	0,99	0,56	—
10343	22	6	7	2	1	2	0	40
D/m	0,16	0,18	0,66	0,09	0,66	0,09	0,80	—
10344	14	5	5	2	2	1	0	29
D/m	0,87	0,50	0,50	0,56	0,56	0,32	0,67	—
10345	30	3	1	0	2	3	1	40
D/m	2,39	1,19	2,10	1,40	0,10	0,85	0,47	—
10346	3	1	2	1	0	3	0	10
D/m	1,67	0,36	0,54	0,79	0,70	3,77	0,40	—
10347	19	6	11	1	3	1	1	42
D/m	1,44	0,04	2,26	0,71	0,75	0,71	0,42	—
10348	18	2	2	2	3	0	1	28
D/m	0,86	1,05	1,05	0,62	1,51	1,17	0,85	—
Summen:	365	84	92	26	28	36	9	640
Erwartet:	360	90	90	30	30	30	10	—
D/m für 36: :9:9:3:3: :3:1.....	0,40	0,68	0,23	0,75	0,37	1,12	0,32	—

TABELLE 21. *F_2 der Kreuzung CIII: L. 25, Bister × L. 26, Schwarz.*
(D/m berechnet für das theoretische Spaltungsverhältnis 9 : 3 : 3 : 1.)

Nr.	Schwarz	Kastanien-braun	Mineral-braun (dunkel)	Bister	Summe
10301	8	3	2	0	13
D/m	0,36	0,40	0,31	0,93	—
10302	23	7	3	3	36
D/m	0,93	0,11	1,60	0,52	—
10303	17	8	7	1	33
D/m	0,55	0,81	0,36	0,76	—
10304	17	4	3	1	25
D/m	1,18	0,35	0,87	0,47	—
10305	16	3	3	1	23
D/m	1,29	0,70	0,70	0,38	—
10306	35	6	5	3	49
D/m	2,14	1,17	1,53	0,04	—
10307	25	5	7	3	40
D/m	0,80	1,01	0,20	0,33	—
10308	21	11	12	2	46
D/m	1,45	0,90	1,27	0,53	—
10309	23	1	3	1	28
D/m	2,75	2,06	1,09	0,59	—
10310	20	4	0	1	25
D/m	2,39	0,35	2,40	0,46	—
10311	0	1	0	0	1
D/m	1,12	2,02	0,48	0,30	—
10312	19	6	4	2	31
D/m	0,57	0,09	0,83	0,04	—
10313	36	10	7	2	55
D/m	1,38	0,11	1,14	0,80	—
10314	24	3	7	3	37
D/m	1,06	1,66	0,03	0,47	—
10315	7	4	1	1	13
D/m	0,17	1,11	1,02	0,22	—
10316	29	9	12	2	52
D/m	0,07	0,27	0,80	0,67	—
10317	17	6	6	2	31
D/m	0,14	0,08	0,08	0,04	—
10318	31	7	12	5	55
D/m	0,02	1,14	0,58	0,87	—
10319	32	8	3	4	47
D/m	1,64	0,30	2,18	0,64	—
10320	30	7	14	6	57
D/m	0,55	1,25	1,12	1,33	—

Nr.	Schwarz	Kastanien-braun	Mineral-braun (dunkel)	Bister	Summe
10321	35	5	4	5	49
D/m	2,14	1,53	1,90	1,15	—
10322	8	1	2	1	12
D/m	0,73	0,93	0,19	0,30	—
10323	8	3	1	2	14
D/m	0,08	0,25	1,12	1,22	—
10324	10	1	3	1	15
D/m	0,81	1,20	0,13	0,06	—
10325	12	4	3	3	22
D/m	0,16	0,07	0,61	1,43	—
Summen: ...	503	127	124	55	809
Erwartet: ...	455,06	151,69	151,69	50,56	—
D/m für 9 : 3 : : 3 : 1	3,38	2,22	2,50	0,65	—

gesamte Individuenanzahl in F_2 betrug 640. Der höchste Wert für D/m für obige Spaltungszahlen erreichte 1,12. Im übrigen vergleiche Tabelle 20, in der auch die Werte von D/m für die Nachkommen jedes F_1-Individuums angegeben sind.

Da wir in Kreuzung Nr. IV in bezug auf die Testafarbe zweifellos ganz dieselben Spaltungsverhältnisse vor uns haben wie in Kreuzung Nr. II, glaube ich von einer weiteren Erörterung derselben Abstand nehmen zu können und verweise diesbezüglich auf die Besprechung der letztgenannten Kreuzung.

KREUZUNG NR. CIII. TESTAFARBE BISTER × SCHWARZ.

Als Eltern zu dieser Kreuzung wurden gleichfalls zwei reine Linien benutzt, von denen die eine identisch mit der in Kreuzung Nr. IV erwähnten »Braunen Bohne» ist, also L. 25. Die zweite Linie, L. 26, stammt, wiederum wie in Kreuzung Nr. IV, aus der Wachsbohne »Merveille du Marché». Die in letzterer Kreuzung verwendete Linie aus »Merveille du Marché», L. 24, ist phänotypisch anscheinend in allen Hinsichten mit L. 26 identisch. Ich verweise daher hier auf die kurze Beschreibung unter Kreuzung Nr. IV. Die Kreuzungsergebnisse haben indessen dargetan, dass zwischen diesen beiden Linien (L. 24 und L. 26) hinsichtlich der Testafarbe ein genotypischer Unterschied vorhanden ist.

Die Kreuzungen wurden auch hier in beiden Richtungen in den

Jahren 1928 und 1929 ausgeführt. In F_1 wurden in bezug auf Testa-, Blüten- und Hülsenfarbe ganz dieselben Beobachtungen gemacht wie in den beiden oben besprochenen Kreuzungen Nr. II und IV. Es dominierte also die grüne Hülsenfarbe über die gelbe, die schwarze Testafarbe über Bister und die dunklere Blütenfarbe Bischofsviolett über die hellere Laeliafarbig.

Die auf F_2 erhaltenen Samen zeigten in bezug auf die Farbe der Samenschale die in Tabelle 21 mitgeteilten Spaltungsresultate. Wie aus dieser Tabelle ersichtlich wurde annähernd folgendes theoretisches Spaltungsverhältnis erhalten: 9 Schwarz : 3 Kastanienbraun : 3 Mineralbraun : 1 Bister. Wir haben also hier zum Unterschied von den früher besprochenen Kreuzungen Nr. II und IV nach Kreuzung von bister × schwarze Testafarbe eine bifaktorielle Spaltung erhalten. Zweifellos besitzen hier beide Eltern den Faktor *G*. Dann erscheint ja eine Ausspaltung der Testafarben Veilchenviolett, Münzbronze und Schamois ausgeschlossen. Wir erhalten also für die beiden Elternlinien folgende Formeln:

L. 25: *PP CC JJ GG bb vv*,
L. 26: *PP CC JJ GG BB VV*.

Bei Umrechnung der in F_2 tatsächlich erhaltenen Spaltungszahlen auf die Kombinationszahl 16 für eine bifaktorielle Spaltung bekommen wir: $9{,}_{95} : 2{,}_{51} : 2{,}_{45} : 1{,}_{09}$. Es ist also hier ein gewisses Defizit für die Farben Kastanienbraun : Mineralbraun vorhanden. Dies würde für eine schwache Koppelung zwischen den Faktoren *B* und *V* sprechen. Bei Betrachtung der Zahlen in Tabelle 3, die dieselbe bifaktorielle Spaltung von Schwarz *PP CC JJ GG Bb Vv* in F_3 und F_4 der Kreuzung Nr. II wiedergibt, finden wir indessen kein solches Defizit. Es mag daher zweifelhaft erscheinen ob man es hier wirklich mit einer schwachen Koppelung oder einer anderen Komplikation zu tun hat. Jedenfalls ist das vorliegende Material zu einer sicheren Beantwortung dieser Frage ganz ungenügend. Diese Frage soll in einer speziell hierauf abzielenden Kreuzung aufgegriffen werden.

In bezug auf die vorliegende Kreuzung Nr. CIII soll schliesslich noch folgendes erwähnt werden. Es wurden, wie zu erwarten war, keine Samen mit chromgrün-schwarzer Testafarbe erhalten. Dieser kommt ja, wie früher nachgewiesen worden ist, die Formel *PP CC JJ gg Bb Vv* zu, die hier — da beide Eltern den Faktor *G* besitzen — nicht erhalten werden konnte. Dies bildet eine weitere Bestätigung der oben für die verschiedenen Testafarben angenommenen genotypischen Konstitution.

SPONTANE KREUZUNGEN MIT SCHWARZSAMIGER MUTTERSORTE.

Unter den zahlreichen spontanen Bohnenkreuzungen, deren Aufspaltungen ich in den Jahren 1927—1929 untersucht habe, befanden sich auch solche, die in der schwarzsamigen Sorte *Flageolet Wachs* angetroffen worden sind. Die Firma W. WEIBULL, Landskrona, hat mir in entgegenkommender Weise eine grössere Menge Samen überlassen, die aus mehreren Tausend kg der genannten Sorte wegen mehr oder weniger abweichender Testafarbe ausgelesen worden sind. Unter diesen befanden sich teils missfarbige schwarze Samen, teils solche mit den Farben Kastanienbraun, Mineralbraun, Veilchenviolett, Münzbronze, Bister und Schamois. Diese Farbenreihe entsprach also gerade der in meinen Kreuzungen Nr. II und IV erhaltenen. Beim Anbau dieser Samen wurden Spaltungen beobachtet, die wir in F_3 und F_4 von Kreuzung II gefunden haben. Die erhaltenen Spaltungszahlen waren meistens klein, doch zeigten sie durchweg gute Übereinstimmung mit jenen von Kreuzung II. Unten werden einige solche Spaltungsverhältnisse mitgeteilt, wobei in Klammern die Nr. der Tabelle angegeben wird, in der die entsprechende Spaltung für F_3 bzw. F_4 von Kreuzung II zu finden ist.

33 Schwarz- und Chromgrün-Schwarz : 9 Veilchenviolett : 5 Münzbronze : 2 Schamois (Tab. 4). D/m für 9 : 3 : 3 : 1 = 1,56, 0,07, 1,53, 0,64.

66 Schwarz : 26 Kastanienbraun (Tab. 7). D/m für 3 : 1 = 0,72.

21 Schwarz : 11 Mineralbraun (Tab. 8). D/m für 3 : 1 = 1,65.

22 Schwarz : 7 Veilchenviolett (Tab. 9). D/m für 3 : 1 = 0,11.

19 Mineralbraun : 5 Münzbronze (Tab. 15). D/m für 3 : 1 = 0,47.

20 Bister : 6 Schamois (Tab. 19). D/m für 3 : 1 = 0,12.

Auf Grund der oben angeführten Ergebnisse ist es wahrscheinlich, dass wir es im vorliegenden Falle mit der fortgesetzten Spaltung eines Bastarden der Formel *PP CC JJ Gg Bb Vv* in F_3, F_4 u. s. w. zu tun haben. Ob der Sorte *Flageolet Wachs* für die Testafarbe die Formel *PP CC JJ gg BB VV* oder *PP CC JJ GG BB VV* zukommt, kann auf Grund obiger Resultate nicht sicher entschieden werden. Ist die Kreuzung mit einer »Braunen Bohne» mit der Testafarbe Bister erfolgt, dann haben wir mit der ersten Formel zu rechnen, was wohl das wahrscheinlichste ist, da Braune Bohnen häufig gebaut werden. Andererseits ist nicht ausgeschlossen, dass eine Kreuzung mit einer Schamois gefärbten Sorte, von denen es ja mehrere im Handel gibt, stattgefunden hat.

KREUZUNG NR. XII. TESTAFARBE ROHSEIDENGELB × GESCHWEFELTES WEISS.

Als Eltern zu dieser Kreuzung wurden zwei reine Linien, L. 27 und L. 29 verwendet. L. 27 stammt aus der französischen Sorte »de Digoin», L. 29 aus »de la Chine». Beide Eltern haben typisch niedrigen Wuchs und weisse Blütenfarbe. L. 27 ist eine Wachsbohne mit deutlich gekrümmten Hülsen. Die Samen dieser Linie sind rohseidengelb mit bister Hilumrand und haben einen mehr oder weniger deutlichen grauen Streifen über der Radicula (ausgehend von der Mikropyle) und sind glänzend. L. 29 hat gerade Hülsen von mittelgrüner Farbe. Die Testafarbe dieser Linie ist Geschwefeltes Weiss. Der Hilumrand ist weiss. Die Samenschale dieser Linie ist häufig mehr oder weniger matt. Hier soll nur die Vererbung der Testafarbe — ohne Berücksichtigung des grauen Streifens — behandelt werden.

Kreuzungen zwischen diesen beiden Linien sind während den Jahren 1928 und 1929 in beiden Richtungen ausgeführt worden. Das hier mitgeteilte Material betrifft F_2 der beiden Jahre 1930 und 1931, zusammen 1289 Individuen, sowie F_3 des Jahres 1931. Die Spaltungsresultate in F_2 sind in Tabelle 22, diejenigen in F_3 in Tabelle 23 zusammenfassend wiedergegeben.

An F_1 konnte folgendes beobachtet werden. Es wurden durchweg typisch niedrige, weissblühende Pflanzen erhalten. Es dominierte die Hülsenfarbe von L. 29, Grün, anscheinend vollkommen über die gelbe Hülsenfarbe von L. 27. Die auf F_1 erhaltenen Samen hatten durchweg marmorierte Samenschale, und zwar Schamois auf Rohseidengelb. Die Samenformen der F_2-Samen zeigten eine gewisse Variation, die indessen bedeutend geringer war, als man auf Grund des Unterschiedes in der Samenform zwischen den beiden Eltern hätte erwarten können.

Die auf F_2 erhaltenen Samen zeigten betreffs der Testafarbe eine klare bifaktorielle Spaltung. Die in Tabelle 22 hierfür mitgeteilten Zahlen stimmen gut mit dem theoretischen Verhältnis 9 Schamois : 3 Rohseidengelb : 3 Geschwefeltes Weiss : 1 Weiss. Die entsprechenden auf die Kombinationszahl 16 berechneten Zahlen sind $8{,}_{65} : 3{,}_{26} : 2{,}_{91} : 1{,}_{18}$. Die für D/m erhaltenen Werte liegen sämtlich unter 2, zeigen demnach statistische Sicherheit an.

Wie aus dem Kopf von Tab. 22 zu entnehmen ist, wurden die Zahlen für die marmorierten mit jenen der entsprechenden einheitlich gefärbten vereinigt. Dies geschah da die Frage nach der Vererbung der Marmorierung in dieser Arbeit keinem eingehenderen Studium unter-

TABELLE 22. *F_2 der Kreuzung XII: L. 27, Rohseidengelb × L. 29, Geschwefeltes Weiss.*

Nr.	Schamois einfarbig und Schamois/Rohseidengelb marmoriert	Rohseidengelb	Geschwefeltes Weiss einfarbig und Geschwefeltes Weiss/Weiss marmoriert	Weiss	Summe
10631	5	3	1	—	9
10632	11	1	—	1	13
10633	2	1	—	—	3
10634	2	—	1	—	3
10635	20	10	7	1	38
10636	4	1	—	—	5
10637	4	4	—	—	8
10638	16	4	7	—	27
10639	3	2	1	1	7
10640	13	1	7	3	24
10641	1	—	2	—	3
10642	1	2	7	2	12
10643	6	1	2	—	9
10644	17	6	4	—	27
10645	7	5	3	2	17
10646	5	3	3	—	11
10647	2	3	1	—	9
10648	8	4	3	1	16
10649	7	2	5	2	16
10650	5	—	4	—	9
10651	4	1	1	2	8
10652	16	2	7	2	27
10653	3	1	—	—	4
10654	9	3	1	1	14
10655	8	4	2	—	14
10656	6	9	2	2	19
10657	7	4	3	3	17
10658	4	4	4	1	13
10659	9	3	4	1	17
10660	17	1	2	—	20
10661	5	1	1	1	8
10662	14	5	9	2	30
10663	5	—	1	—	6
10664	5	6	4	1	16
10665	20	4	3	1	28
10666	4	—	1	2	7
10667	5	3	—	—	8
10668	9	6	1	1	17
10669	5	1	—	1	7

Nr.	Schamois einfarbig und Schamois/Rohseidengelb marmoriert	Rohseidengelb	Geschwefeltes Weiss einfarbig und Geschwefeltes Weiss/Weiss marmoriert	Weiss	Summe
10670	7	—	1	—	8
10671	4	6	3	4	17
10672	18	8	2	1	29
10673	20	12	4	2	38
10674	2	1	2	—	5
10675	14	7	5	5	31
10676	4	2	3	1	10
10677	10	6	3	6	25
10678	5	4	4	1	14
10679	2	3	3	—	8
10680	9	4	1	—	14
10681	3	2	6	2	13
10682	15	5	3	2	25
10683	2	2	1	—	5
10684	—	5	1	2	8
10685	8	16	8	2	34
10686	1	2	1	—	4
10687	5	3	1	1	10
10688	6	4	1	1	12
10689	13	7	2	1	23
10690	8	1	5	1	15
10691	16	6	6	—	28
11711	13	15	6	3	37
11712	14	3	1	1	19
11713	8	5	9	1	23
11714	19	3	7	3	32
11715	19	12	6	2	39
11716	15	12	10	1	38
11717	22	9	2	4	37
11718	18	3	3	3	27
11719	17	10	5	3	35
11720	15	5	6	5	31
11721	17	8	6	2	33
11722	13	1	4	1	19
Summen: ...	696	263	235	95	1289
Erwartet: ...	724,50	241,95	241,95	80,60	—
D/m für 9:3:3:1.....	1,57	1,50	0,50	1,64	—

zogen werden soll. Werden die in Rede stehenden marmorierten Typen von den entsprechenden ganzfarbigen getrennt, erhält man die

TABELLE 23. *Spaltungsresultate in F_2 der Kreuzung XII: L. 27, Rohseidengelb × L. 29, Geschwefeltes Weiss.*

F_2		Spaltung in F_3					
Testafarbe	Formel	Schamois einfarbig	Schamois/ Rohseidengelb marmoriert	Rohseidengelb	Geschwefeltes Weiss einfarbig	Geschwefeltes Weiss/ Weiss marmoriert	Weiss
Schamois einfarbig	*PP CC JJ*	116 (konstant)	—	—	—	—	—
Schamois einfarbig	*PP CC Jj*	131	—	—	54	—	—
D/m für 3 : 1		1,15					
Schamois/Rohseidengelb marmoriert	*PP Cc JJ*	84	167	86	—	—	—
D/m für 1 : 2 : 1		0,93	0,16	0,22			
Schamois/Rohseidengelb marmoriert	*PP Cc Jj*	87	165	83	26	63	41
D/m für 3 : 6 : 3 : 1 : 2 : 1		0,92	0,88	0,49	0,59	0,68	2,28
Rohseidengelb	*PP cc JJ*	—	—	162 (konstant)	—	—	—
Rohseidengelb	*PP cc Jj*	—	—	195	—	—	72
D/m für 3 : 1				0,74			
Geschwefeltes Weiss einfarbig	*PP CC jj*	—	—	—	45 (konstant)	—	—
Geschwefeltes Weiss / Weiss marmoriert	*PP Cc jj*	—	—	—	15	26	13
D/m für 3 : 1					0,47	0,27	0,16
Weiss	*PP cc jj*	—	—	—	—	—	26 (konstant)

folgende Verteilung der 1289 F_2-Individuen: 215 Schamois: 481 Schamois/Rohseidengelb marmoriert : 263 Rohseidengelb: 74 Geschwefeltes Weiss: 161 Geschwefeltes Weiss/Weiss marmoriert: 95 Weiss, welches Verhältnis gut mit dem theoretischen Verhältnis 3:6:3:1:2:1 übereinstimmt. Bei einer Umrechnung der erhaltenen Zahlen auf die Kombinationszahl 16 resultiert nämlich folgende Proportion: 2,67 : 5,95 : 3,27 : 0,92 : 2,00 : 1,18. Auch liegen alle Werte für D/m unter 2 (der höchste Wert hat 1,91 betragen).

Hier soll eine gewisse Schwierigkeit bei der Beurteilung der Testafarbe in vorliegender Kreuzung erwähnt werden. Wie schon im Kapitel über die hier spaltenden Testafarben angeführt worden ist, können schlecht ausgereifte Samen von Rohseidengelb leicht mit schlecht ausgereiften Samen von Schamois verwechselt werden und umgekehrt. Ich habe hier, um einen eventuellen Einfluss solcher fehlerhafter Beurteilung festzustellen, eine Berechnung der Spaltungszahlen nach den gleichen Prinzipien wie in Tab. 22, jedoch nur mit solchen Nummern ausgeführt, in denen gar keine schlecht ausgereiften Samen vorgekommen sind. Hierbei wurde folgendes Verhältnis erhalten: 364 Schamois : 123 Rohseidengelb : 131 Geschwefeltes Weiss : 44 Weiss. Berechnet auf 16 resultiert das Verhältnis 8,80 : 2,98 : 3,16 : 1,06. Während in Tab. 22 die Werte für D/m zwischen 1,64 und 0,50 variierten, liegen sie hier zwischen 0,68 und 0,11, also eine viel bessere Annäherung an das erwartete Verhältnis 9 : 3 : 3 : 1 anzeigend. Dieser Umstand spricht dafür dass die im ersteren Falle höheren Werte für D/m ausschliesslich auf Schwierigkeiten bei der Beurteilung von schlecht ausgereiften Samen zurückzuführen sind.

Offenbar dürfte schon die in F_2 konstatierte Spaltung genügen um die Genenkonstitution für die Testafarben der beiden Elternlinien angeben zu können. Da beide Linien gefärbte Samenschale haben, müssen sie den Grundfaktor für die Ausbildung von Farbe, *P*, enthalten. Die eine Elternlinie enthält einen Farbenfaktor, *C*, für Geschwefeltes Weiss, die andere einen Farbenfaktor, *J*, für Rohseidengelb. Die Formel für den Bastarden sollte demnach sein: *PP Cc Jj*. Durch das Zusammenwirken von *C* und *J* kommt es zur Ausbildung einer dritten Farbe: Schamois. Der Bastard erwies sich als marmoriert: Schamois auf Rohseidengelb. Die Spaltung in F_2 zeigt, dass der eine der beiden Farbenfaktoren, nämlich *C*, in heterozygotischer Dosis die Marmorierung der Testa bedingt. Dass der andere Faktor *J* in heterozygotischer Dosis keine Marmorierung verursacht geht daraus hervor, dass keine Marmorierten Rohseidengelb/Weiss ausgespaltet haben. Samen nur mit dem Grundfaktor *P* haben weisse Testa.

Die oben auf Grund der Spaltung in F_2 angenommenen Konstitutionen sind durch die Ergebnisse in der dritten Generation durchweg einwandfrei bestätigt worden (siehe Tabelle 23). Der Übersichtlichkeit halber teile ich hier ein Spaltungsschema mit, wobei nur die beiden spaltenden Farbenfaktoren *C* und *J* berücksichtigt werden.

F_1	Spaltung in F_2		Spaltung in F_3
	1 *CC JJ*	Schamois einfarbig	Konstant
	2 *CC Jj*	Schamois einfarbig	3 Schamois : 1 Geschwefeltes Weiss
Cc Jj	2 *Cc JJ*	Schamois/Rohseidengelb marmoriert	1 Schamois : 2 Schamois/Rohseidengelb marmoriert : 1 Rohseidengelb
Schamois/Rohseidengelb marmoriert	4 *Cc Jj*	Schamois/Rohseidengelb marmoriert	3 Schamois : 6 Schamois/Rohseidengelb marmoriert : 3 Rohseidengelb : 1 Geschwefeltes Weiss : : 2 Geschwefeltes Weiss/Weiss marmoriert : 1 Weiss
	1 *cc JJ*	Rohseidengelb	Konstant
	2 *cc Jj*	»	3 Rohseidengelb : 1 Weiss
	1 *CC jj*	Geschwefeltes Weiss	Konstant
	2 *Cc jj*	Geschwefeltes Weiss/Weiss marmoriert	1 Geschwefeltes Weiss : 2 Geschwefeltes Weiss/Weiss marmoriert : 1 Weiss
	1 *cc jj*	Weiss	Konstant

Die in F_3 erhaltenen Spaltungszahlen stehen durchgehend in Übereinstimmung mit obigem Spaltungsschema. Diese Spaltungsergebnisse haben ihr ganz besonderes Interesse durch die Ausspaltung der weissen Samen, die in einwandfreier Weise dartun, dass der *Grundfaktor P an und für sich keine Färbung der Testa verursacht.* Die hier erhaltenen weissen Samen, die demnach ausser dem Grundfaktor *P* keinen anderen Farbenfaktor enthalten dürften, werden ein Kreuzungsmaterial von grösster Bedeutung für die weitere Aufklärung der Genenkonstitution verschiedener Testafarben liefern.

DISKUSSION EINIGER RESULTATE FRÜHERER FORSCHER IM LICHTE DER HIER VORGELEGTEN KREUZUNGSERGEBNISSE.

Bevor ich an die Besprechung von Kreuzungsresultaten schreite, die hinsichtlich verschiedener Farben mit den hier vorgelegten Daten in Einklang gebracht werden können, sollen die *bisherigen Auffassungen über den Grundfaktor* für die Ausbildung von Testafarbe zusammenfassend erörtert werden.

Die ersten Arbeiten, die für das Vorhandensein eines Grundfaktors sprechen, sind die von VON TSCHERMAK (1902 und 1904). In diesen wurde festgestellt, dass bei Kreuzung von weissen Bohnen mit pigmentierten in F_2 stets eine Spaltung von 3 Pigmentiert : 1 Weiss stattfand, wobei die pigmentierten selbst in mehrere Farben spalten konnten. Dieses Spaltungsresultat deutet darauf hin, dass es ausser einem oder mehreren Farbenfaktoren einen Faktor geben muss — den Grundfaktor —, bei dessen Abwesenheit es überhaupt nicht zu einer Ausbildung von Testafarbe kommen kann. Weiteres über den Grundfaktor für Testafarbe ist aus diesen Arbeiten VON TSCHERMAKS nicht zu entnehmen.

Die ersten Arbeiten von EMERSON (1902 und 1904) enthalten nichts über einen Grundfaktor für die Ausbildung von Farbe in der Samenschale.

SHULL hat in seinen Arbeiten (1907 a, 1907 b und 1908) die Anwesenheit von »latenten Charakteren» (Farbenanlagen) in weissen Bohnen konstatiert. SHULL, dessen Arbeiten von 1907 b und 1908 schon im Sinne der Faktorenlehre geschrieben sind, nimmt nun an, dass sich diese (latenten) Anlagen infolge des Fehlens eines Grundfaktors für die Ausbildung von Testafarbe nicht äussern, und verwendet als erster als Symbol für diesen den Buchstaben *P* (1907 b, S. 829). SHULL hat gleichwie VON TSCHERMAK eine Spaltung von 3 Pigmentiert : 1 Weiss gefunden, wobei Pigmentiert selbst in mehrere Farben gespaltet hat. SHULL stellt für die verschiedenen ausspaltenden Samenfarben Formeln auf, aus denen hervorgeht, dass der Grundfaktor *P* nicht nur Bedingung für die Bildung von Pigment überhaupt sein soll, sondern dass dieser überdies eine hellbraune oder gelbe Farbe der Samenschale verursacht. Das ist aber nur eine Annahme, denn ein Beweis hierfür kann in den genannten Arbeiten von SHULL nicht gefunden werden. Es können ja beide von ihm verwendeten Elternsorten einen gemeinsamen vierten Faktor (oder mehrere solche) für das erwähnte Hellbraun besessen haben. Auch dann

wird SHULLS *P b m* hellbraun, während gleichzeitig an den Spaltungsverhältnissen der übrigen Testafarben nichts geändert wird.

Diese Vermutung SHULLS, dass der Grundfaktor *P* selbst eine hellbraune-gelbliche Testafarbe verursacht, finden wir später von verschiedenen Verfassern ohne Kritik übernommen, bis sie schliesslich — wie wir sehen werden — in der Literatur als »konstatiert» figuriert.

EMERSON (1909) findet gleichfalls dass Pigmentiert über Weiss dominiert und dass in allen Kreuzungen zwischen Weiss und Pigmentiert in F_2 eine Abspaltung von $^1/_4$ Weiss stattfindet. EMERSON (l. c. S. 75) bezeichnet Anwesenheit von Pigment durch *P*, Abwesenheit von Pigment durch *p*. Wir finden hier die gleiche Annahme wei bei SHULL, indem *P* schon allein eine Testafarbe verursachen soll.

EMERSON erörtert (l. c. S. 95 ff.) auch die Möglichkeit, dass Samen nur mit dem Grundfaktor *P* weiss sein können und führt hierzu zwei Beispiele aus der Literatur an. In diesen beiden Fällen handelte es sich aber nicht um Kreuzungen zwischen verschiedenen Rassen von *Phaseolus vulgaris* sondern um Kreuzungen zwischen *Phaseolus multiflorus* var. *coccineus* mit *Ph. vulgaris*. Der eine Fall betrifft VON TSCHERMAKS (1904) Kreuzung von Wachsdattel mit »gelbbraunen» Samen mit Scarlet Runner mit »schwarz/lilarosa» marmorierten Samen. Die F_2-Samen zeigten sehr dunkle Farben, die F_3-Samen zeigten wenigstens 11 verschiedene hellere und dunklere Farben und in F_4 schliesslich spalteten mehrere weisssamige Individuen aus. Der zweite Fall betrifft HALSTEDS (1906, 1907) Kreuzung zwischen Tennesee Green mit »hellbraunen» Samen und Scarlet Runner, in der in F_3 Individuen mit weissen Samen ausspalteten. Dass die Ergebnisse dieser Artkreuzungen indessen nicht ohne weiteres zu Schlusssätzen in bezug auf den Grundfaktor für die Testafarbe von *Ph. vulgaris* verwendet werden können, dürfte wohl selbstverständlich sein.

Im Jahre 1912 veröffentlicht VON TSCHERMAK eine grössere Arbeit, die seine bisherigen Kreuzungsergebnisse mit Bohnen im Lichte der Faktorenlehre behandelt. Er bezeichnet in dieser den Grundfaktor für Testafarbe mit *A*, und fasst diesen selbst als Farbe verursachend auf, was u. a. daraus hervorgeht, dass er der Gelben Prinzessbohne die Genenkonstitution *A b c m* beilegt (l. c. S. 192). Da die Gelbe Prinzessbohne durch die Testafarbe Bister charakterisiert ist, sollte also laut VON TSCHERMAK der Grundfaktor allein diese Farbe hervorrufen.

SHAW und NORTON (1918) bringen in dieser ihrer Arbeit eine Notiz, die klar darauf hinzudeuten scheint, dass der Grundfaktor für Testafarbe, *P*, selbst keine Farbe der Samenschale verursacht. Sie schreiben

Seite 65: »The appearance of pigment in the seed coat of beans is usually the expression of a complex factor or the concurrence of several factors. In the absence of any one of the elements of this factor complex the beans are unpigmented. If this be the case, crosses of non-pigmented beans may give rise to pigmented offspring. One such cross has been encountered in this work, that of Davis Wax × Michigan White Wax.»

Merkwürdigerweise erwähnen SHAW und NORTON nichts mehr über diese wohl sehr wichtige Kreuzung. Sie wurde anscheinend in F_2 nicht untersucht und die Verfasser scheinen ihr dann auch nicht mehr Bedeutung in obigem Sinne beigelegt zu haben, denn später (l. c. S. 73) wird teils EMERSONs Annahme der Farbenwirkung des Grundfaktors *P* kritiklos übernommen, teils geht aus mehreren Stellen ihrer Arbeit deutlich hervor, dass sie den Grundfaktor *P* selbst auch als Farbe verursachend betrachten. So heisst es in ihrem Kapitel »The Inheritance of Pigments» (l. c. S. 84): »The production of a totally pigmented bean, then, rests on the presence of several factors. First, we must have *P*, in the absence of which we have a white bean; second, *T*, in the absence of which the bean has an eye; third, the presence of *M* or *M'*, the former causing beans of the yellow-black series, and the latter, pigment of the red series ... If *P* and *T* are present and *M* and *M'* absent, the bean is buff-colored.» Das Gen *T* verursacht also laut SHAW und NORTON Ganzfarbigkeit der Samenschale, bei *t* ist die Samenschale nur zum Teil gefärbt. *M* und *M'* sollen zwei Gene sein, welche die Ausbildung zweier verschiedener Serien von Testafarben bedingen, selbst aber keine Farbe hervorrufen. Alle in meinen hier besprochenen Kreuzungen vorkommenden Typen sollten demnach die Gene *T* und *M* enthalten. Bezüglich der Existenz der Gene *M* und *M'* will ich mich einstweilen skeptisch verhalten.

SHAW und NORTON schreiben weiter (l. c. S. 84): »When the factors *P*, *T* and *M* are present, a buff or ecru colored bean is produced». Seite 86 (l. c.) heisst es dann: »In other crosses of this table buff-colored beans (B) appear. According to our hypothesis this can occur only when the modifier *M* is absent, or, if present, only when all determiners are absent».

Aus Obenstehendem geht klar hervor, dass der Grundfaktor *P* allein laut den genannten beiden Verf. Ecru (= Schamois) oder wenigstens eine ähnliche Farbe bedingen soll. Erwähnt sei hier noch, dass die mir zur Verfügung stehenden Proben von Davis Wax (erhalten aus U. S. A.) einen gelben Ring um das Hilum aufweisen. Diese Sorte könnte demnach sowohl den Grundfaktor und einen oder mehrere Farbenfaktoren

enthalten, aber es müssten ihr der oder die Faktoren für Ganzfarbigkeit fehlen. Dann könnte das Erscheinen von gefärbten Bohnen in F_1 der oben erwähnten Kreuzung von SHAW und NORTON — wenn es nicht auf spontane Kreuzung beruht? — auf die Anwesenheit des Faktors für Ganzfarbigkeit, *T*, in der anderen Elternsorte zurückzuführen sein. Eine Wiederholung dieser Kreuzung soll hier Klarheit schaffen.

KOOIMAN (1920) hat in einer umfangreicheren Arbeit die Resultate einer Kreuzung zwischen den beiden holländischen Bohnensorten »Bruine boon» und »Dubbele Hollandsche Spersieboon» vorgelegt, die laut ihm eine Spaltung in sechs Faktoren zeigen soll. Seine F_2-Generation bestand aus 212 Individuen, die eine Spaltung von 154 verschieden Pigmentiert : 58 Weiss zeigten. Eine auf den Grund gehende Klarlegung einer Spaltung, an der sechs Faktoren teilnehmen, erscheint bei dieser Individuenanzahl wohl ausgeschlossen. KOOIMAN, der seinen Grundfaktor für Testafarbe mit *A* bezeichnet, ist der Ansicht, dass dieser selbst keine Farbe verursacht. Als Beweis hierfür stützt er sich teils auf die oben erwähnte Notiz von SHAW und NORTON in bezug auf das Erscheinen von gefärbten Bohnen in F_1 nach Kreuzung von zwei weisssamigen Rassen (vgl. die dortige Diskussion), teils auf die Abspaltung von weissen Bohnen in F_3 und F_4 seiner Kreuzung. In diesen wurde nämlich in 10 Serien zusammen eine Spaltung von 84 Gefärbt : 44 Weiss erhalten. Diese Zahlen sagen aber nichts Sicheres darüber aus, dass es sich hier nicht um eine monofaktorielle Spaltung handelt. D/m beträgt für dieses Verhältnis nämlich 2,45.

SIRKS (1920) berichtet über die Analyse einer spontanen Bohnenkreuzung. Auf Grund der erhaltenen Spaltungsresultate sagt er in seiner Zusammenfassung in bezug auf den Grundfaktor *P* folgendes : 1. *P* ist der Grundfaktor für das Zustandekommen von Farbe; allein verursacht dieser Faktor die Farbe Schamois; seine Abwesenheit bedingt weisse Testafarbe, unabhängig von der eventuellen Anwesenheit von anderen Farbenfaktoren. Und 2. *G* ist ein Faktor für gelbbraune Farbe der Bohnen, der die Schamois-Farbe von *P* in Gelbbraun umwandelt. Hier haben wir also schon die sichere Feststellung der eigenen Farbenwirkung von *P*, trotzdem hierfür kein Beweis erbracht wird.

MACHLEJD (1926) bespricht die Ergebnisse von vier Kreuzungen, in denen er die Vererbung der Testafarbe studiert. Er bezieht die Farben auf Farbenfelder im Code des Couleurs von KLINCKSIECK et VALETTE. Der eine Elter in allen seinen vier Kreuzungen ist *Phaseolus melleus*, dessen Samenschale Schamois gefärbt ist. MACHLEJD bezeichnet diese Farbe als »sand colour» und bezieht sie auf CC 153D (vgl. meine Be-

schreibung von Schamois). In bezug auf die genetische Konstitution dieser Farbe sagt er (l. c. S. 68): »Factor *P* indicates the sand colour». Auch bei MACHLEJD erscheint also eine Farbenwirkung durch *P* allein sicher.

Und schliesslich finden wir folgende Äusserung bei E. NILSSON (1929): »Als Grundfaktor für Schalenfarbe haben LUNDBERG und ÅKERMAN (1917), SIRKS (1920), SHULL (1908) und SHAW und NORTON (1918) einen Faktor konstatiert, der von diesen Autoren mit *P* bezeichnet wird, und der, wie es scheint, den Grund für den gleichen Phänotypus bildet, der den abweichenden, rezessiven Teil meines Materials »(Schamois)» kennzeichnet». Hier wird also das Konstatieren der Farbenwirkung des Grundfaktors *P* seitens sechs Autoren angeführt. Von diesen haben übrigens zwei, LUNDBERG und ÅKERMAN (1917), gar nichts über einen Grundfaktor erwähnt.

Die obige Übersicht über die bisherigen Auffassungen hinsichtlich des Effektes des Grundfaktors für die Ausbildung von Testafarbe bei *Phaseolus vulgaris* dürfte die auf diesem Gebiete herrschende Unklarheit zur Genüge beleuchtet haben. Wir entnehmen aus dieser Übersicht, dass die Mehrzahl der Forscher die Ansicht vertreten haben, dass der Grundfaktor nicht nur Bedingung für die Ausbildung von Farbe überhaupt sei, sondern dass er selbst auch die Ausbildung der Farbe Schamois veranlasst. Ein Forscher (VON TSCHERMAK 1912) hielt die Ausbildung von Bister als durch ihn verursacht. Zwei Forscher (SHAW und NORTON 1918) machen in bezug auf die Wirkung des Grundfaktors widersprechende Angaben, und ein Verfasser schliesslich (KOOIMAN 1920) vermutet — gestützt auf SHAW und NORTON (l. c.) und ohne Beweise hierfür erbracht zu haben — dass dem Grundfaktor selbst keine Farbenwirkung zukomme. Wie in meiner Kreuzung Nr. XII einwandfrei bewiesen worden ist, wird die Farbe Schamois durch das Zusammenwirken von zwei Farbenfaktoren (*C* und *J*) mit dem Grundfaktor *P* verursacht, und dem Grundfaktor allein kommt keine Farbenwirkung zu. Bohnen mit dem Gen *P* allein (ohne weitere Farbenfaktoren) sind weiss. Bei Kreuzung von zwei Bohnenlinien mit verschieden gefärbter Testa, bei denen die betreffende Farbe je nur durch einen Farbenfaktor verursacht wird, also dem Beispiele *PP CC jj* × *PP cc JJ* entprechend, ist daher eine Spaltung in 15 Pigmentiert : 1 Weiss zu erwarten. Und gerade dieses Spaltungsverhältnis ist in meiner Kreuzung Nr. XII realisiert worden.

Nun soll schliesslich eine kurze Übersicht über von anderen Verfassern konstatierte Farbenspaltungen gegeben werden, die mit meinen

hier vorgelegten Spaltungsresultaten in Beziehung gebracht werden können.

LUNDBERG und ÅKERMAN (1917) haben die Nachkommen einer spontanen Kreuzung untersucht. Sie fanden in einem Stamm von »Braunen Bohnen» mit *Schokoladefarbigen* Samen, der im Jahre vorher neben einer Parzelle mit gelbbraunen Prinzessbohnen gewachsen ist, eine Pflanze, die dunkelbraune Samen hatte, im übrigen aber vollständig mit der Muttersorte übereinstimmte.

Es sei erwähnt dass die gelbbraune Prinzessbohne die Testafarbe *Bister* hat, die schwedischen sogenannten »Schokoladefarbigen Bohnen» die Testafarbe *Münzbronze*. Auf Grund obiger Angaben und bei Kenntnis der Resultate meiner Kreuzungen Nr. II und IV können wir schon mit grosser Wahrscheinlichkeit auf das zu erwartende Kreuzungsresultat schliessen. Bister hat die Formel *PP CC JJ GG bb vv*, Münzbronze die Formel *PP CC JJ gg BB vv*. Es ist also ein in bezug auf die Genen *G* und *B* heterozygotischer Bastard, *PP CC JJ Gg Bb vv*, zu erwarten. In F_2 soll es zu einer bifaktoriellen Spaltung nach dem Schema:

9 Mineralbraun : 3 Münzbronze : 3 Bister : 1 Schamois

kommen, ganz wie sie für F_3 und F_4 meiner Kreuzung Nr II in Tabelle 11 mitgeteilt worden ist. LUNDBERG und ÅKERMAN haben auch genau eine solche Spaltung erhalten. Dr. ÅKERMAN hat die Liebenswürdigkeit gehabt Samenproben aus F_3 meiner Kreuzung Nr. II mit Samen aus der erwähnten spontanen Kreuzung zu vergleichen und mir mitgeteilt, dass diese praktisch genommen mit den oben erwähnten Farben identisch sind. Die Farbenbezeichnungen von LUNDBERG und ÅKERMAN »Dunkelbraun, Schokoladefarbig, Gelbbraun und Gelbweiss» entsprechen nach den von mir in vorliegender Arbeit beschriebenen Farben: Mineralbraun, Münzbronze, Bister und Schamois.

JOHANNSEN hat in seinem Lehrbuch »Elemente der exakten Erblichkeitslehre» (1. Aufl. 1909, S. 53; 3. Aufl. 1926, S. 63) die Ergebnisse der Kreuzung einer »gelbsamigen» Bohnenrasse mit einer »schwarzsamigen» mitgeteilt. In F_2 wurden 558 Individuen mit folgenden Spaltungen in bezug auf die Testafarbe erhalten: 293 Schwarz und Schwärzlich : 105 Violett : 121 Bronze : 39 Gelb. Der Bastard soll schmutzig schwarze Samen gehabt haben. Die Spaltung in F_2 war bifaktoriell und hat umgerechnet auf die Kombinationszahl 16 das Verhältnis $8{,}41 : 3{,}01 : : 3{,}46 : 1{,}12$ gegeben.

Ich glaube nicht fehlzugehen wenn ich obiges Kreuzungsergebnis JOHANNSENS als mit der in Tabelle 4 dieser Arbeit mitgeteilten Spaltung von Chromgrün-Schwarz in F_3 und F_4 von Kreuzung Nr. II überein-

stimmend auffasse. In meinem Falle haben wir folgendes theoretisches Spaltungsverhältnis mit folgenden Testafarben:

9 Schwarz und Chromgrün-Schwarz : 3 Veilchenviolett : 3 Münzbronze : 1 Schamois.

Mit den entsprechenden Bezeichnungen JOHANNSENs erhalten wir:

9 Schwarz und Schwärzlich : 3 Violett : 3 Bronze : 1 Gelb.

JOHANNSENs vier Farbenbezeichnungen stimmen sehr gut mit meinen überein. Schamois ist ja nichts anderes als eine bestimmte Art von Gelb. Es dürfte demnach nicht daran zu zweifeln sein, dass es sich in diesen beiden Fällen um eine Spaltung in bezug auf dieselben Genen gehandelt hat. Den von JOHANNSEN als Eltern verwendeten Bohnenrassen sollten also die Formeln

PP CC JJ gg bb vv (Gelb) und *PP CC JJ gg BB VV* (Schwarz) zukommen.

Die oben erwähnte Kreuzung ist von JOHANNSEN als ein Beispiel für Epi- bzw. Hypostasie verwendet worden. JOHANNSEN schreibt (1926, S. 443—444): »Wir können dieses Resultat» [die F_2-Spaltung 9 VB (Schwarz) : 3 Vb (Violett) : 3 vB (Bronze) : 1 vb (Gelb)] »in folgender Weise deuten: Das Gen B bedingt, dass statt gelbe bronzene Färbung auftritt. Diese Farbe ist wahrscheinlicherweise eine Modifikation der gelben Farbe. Das Gen V bedingt violette Färbung, wodurch gelb nicht bemerkt wird. Der violette Farbstoff ist im Zellsaft lokalisiert, der gelbe Farbstoff in den Zellwänden gebunden. Indem hier sowohl Violett als Gelb wirklich existierende Charaktere sind, kann gesagt werden, dass Gelb von Violett gedeckt oder versteckt wird. Ein solches Verhalten hat man mit den Wörtern *Hypostasie* bzw. *Epistasie* bezeichnet. Violett ist Gelb gegenüber epistatisch, Gelb aber hypostatisch im Verhalten zu Violett. Wenn V und B zusammentreffen, wird schwarze Farbe in den Samenschalen gebildet. Violett ist also nicht epistatisch über bronze, sondern bildet damit eine einheitlich hervortretende Summationseigenschaft, gewissermassen eine 'Konstruktion'».

Die Verwendung dieses Kreuzungsresultates als Beispiel für Epi- bzw. Hypostasie erscheint mir nicht angebracht. Epistasie soll ja eine Deckungserscheinung oder eine Nichtrealisierung eines Charakters sein. Die Betrachtung im obigen Beispiel ist rein phänotypisch, aber gar nicht genotypisch. Gelb (Schamois) wird durch gewisse Gene (*C* und *J* zusammen) verursacht, durch ein weiteres Gen (*B*) entsteht Bronze, durch ein anderes (*V*) Violett, durch die Anwesenheit der beiden letzten Schwarz. Wir können demnach im vorliegenden Fall auf Grund der vorhandenen Testafarbe stets darauf schliessen aus welchen Einzel-

farben diese zusammengesetzt ist, bzw. welche Genenkonstellation für die betreffende Farbe verantwortlich ist. Es wird nichts verdeckt. Wird der Epistasie- bzw. Hypostasie-Begriff in diesem Sinne verwendet, dann können wir in allen Fällen wo der phänotypische Effekt eines Gens durch die Anwesenheit eines weiteren abgeändert wird von Epi- bzw. Hypostasie sprechen. Bei *Pisum sativum* z. B. verursacht ein Gen *A* blassrosa Blütenfarbe; kommt ein weiteres Gen *B* hinzu, erhält man bläulichviolette Blütenfarbe. Nach Obigem hätten wir hier einen Fall von Epistasie vor uns. Ich möchte die Erscheinung der Epi- bzw. Hypostasie mehr genotypisch betrachten und sie folgendermassen charakterisieren. Unter Epi- bzw. Hypostasie ist die Erscheinung zu verstehen, dass die An- bzw. Abwesenheit eines Gens (des hypostatischen) auf Grund der Anwesenheit eines anderen Gens (des epistatischen) sich ohne Kreuzungsversuche nicht feststellen lässt. Die durch das hypostatische Gen verursachte (hypostatische) Eigenschaft wird von der durch das epistatische Gen verursachten (epistatischen) Eigenschaft verdeckt. Es können auch mehrere Gene bzw. die durch dieselben bedingten Eigenschaften hypo- bzw. epistatisch sein.

Schöne solche Beispiele für Epi- bzw. Hypostasie finden wir in NILSSON-EHLES (1909, 1911) Kreuzung von schwarz- mit gelbährigem Hafer, in VON TSCHERMAK und BIFFENS Kreuzung von 2- mit 4-zeiliger Gerste u. a. In diesen Fällen fand in F_2 eine Spaltung im Verhältnis 12 : 3 : 1 statt, wobei ein neuer Typus (weissähriger Hafer, sechszeilige Gerste) zutage kam. Ein ähnliches hübsches Beispiel finden wir in meiner obigen Kreuzung Nr. II in bezug auf die Farbe Bister, verursacht durch das Gen *G*. Die beiden Genotypen *PP CC JJ gg BB VV* und *PP CC JJ GG BB VV* haben schwarze Samenschale. Sie sind nicht voneinander zu unterscheiden und auf Grund des Phänotypus kann bei diesen Konstitutionen ohne Kreuzungsversuche nicht festgestellt werden ob die hypostatische Farbe Bister, verursacht durch das hypostatische Gen *G*, vorhanden ist oder nicht. *BB VV*, Schwarz, ist also gegenüber Bister, *GG*, epistatisch.

E. NILSSON (1929) hat in einer Probe der Bohnensorte *Apollo* (Bister) einige Samen mit Schamois Testafarbe gefunden. Von diesen wurden drei Pflanzen erhalten, die dann konstant Schamois Samen gaben. Von der Muttersorte wurden einige heterozygotische Samen gefunden, die in bezug auf Samenfarbe nach dem Verhältnis 3 Bister : 1 Schamois spalteten. Da die Schamois-Samen produzierenden Pflanzen in ihren übrigen Eigenschaften ganz mit denen von *Apollo* (Bister) übereinzustimmen schienen, fasst NILSSON erstere als eine Verlustmuta-

tion auf. Ob dies wirklich der Fall gewesen ist oder nicht darüber kann man sich nicht mit Bestimmtheit äussern. Jedenfalls kommen spontane Kreuzungen nicht selten vor, und es braucht ja nur eine Kreuzung mit einem anderen Biotypus stattzufinden, dem dass Gen *G* für Bister fehlt und der die Gene für Schamois (*C* und *J*) und eventuell noch andere enthält, damit es zur Ausspaltung von Pflanzen mit in bezug auf *G* heterozygotischen Samen kommt. Diese können von den Samenfirmen auf Grund der mit *Apollo* übereinstimmenden Testafarbe Bister aus den Samenernten nicht entfernt werden. Und ich glaube dass man unter einigen Hunderten von solchen sicherlich Typen auffinden dürfte, die sich nur auf Grund okulärer Besichtigung nicht von *Apollo* unterscheiden lassen.

Herr Züchter E. NILSSON hat die Liebenswürdigkeit gehabt mir eine Probe seiner Schamois gefärbten Samen zu überlassen. Diese haben sich als mit meinem Schamois-Typus übereinstimmend erwiesen, weshalb hier kein Zweifel darüber bestehen kann, dass es sich im oben angeführten Falle hinsichtlich Testafarbe um eine Spaltung nach der Formel *PP CC JJ Gg* gehandelt hat.

Die im Vorstehenden besprochenen Kreuzungsresultate anderer Forscher werden durch meine hier vorgelegten Ergebnisse durchweg bestätigt. Die Gene *G*, *B* und *V* scheinen also unabhängig voneinander vererbt zu werden. Laut den von mir in Kreuzung Nr. XII mitgeteilten Resultaten werden auch die beiden Farbenfaktoren *C* und *J* unabhängig voneinander vererbt. Wie sich diese beiden letzten in genannter Hinsicht zu den drei Faktoren *G*, *B* und *V* verhalten bleibt noch festzustellen. Das Gleiche gilt für die Farbenwirkung dieser drei Faktoren im Verhältnis zum Grundfaktor *P* bzw. zu jedem der beiden Farbenfaktoren *C* und *J* für sich.

Schliesslich soll noch erwähnt werden, dass KOOIMAN in seiner Arbeit des Jahres 1920 als erster festgestellt zu haben scheint, dass der Faktor für Geschwefeltes Weiss, *C* (von KOOIMAN mit *B* bezeichnet) in heterozygotischer Dosis Marmorierung der Testafarbe verursacht. Die Farbe wird von KOOIMAN als lichtzitronengelb bezeichnet. Dieser Befund ist durch meine Spaltungsresultate in Kreuzung Nr. XII bestätigt worden. Dass jedoch nur dieser Faktor allein imstande ist in heterozygotischer Dosis Marmorierung der Testafarbe hervorzurufen, glaube ich nicht, da mir u. a. z. B. heterozygotische Typen bekannt sind, die nur eine sehr schwach lichtgraue Marmorierung aufweisen. Der Vererbung der Marmorierung der Testafarbe werde ich in nächster Zeit eine besondere Untersuchung widmen.

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BRASSICA NAPOCAMPESTRIS, A NEW CONSTANT AMPHIDIPLOID SPECIES HYBRID

BY *H. N. FRANDSEN* AND *Ö. WINGE*
TAASTRUP AND COPENHAGEN

I. GENETIC EXPERIMENTS.

(BY H. N. FRANDSEN).

LATELY several investigators have been occupied with the question of the rising of polyploid forms of plants by species crossing, and in the literature several papers have appeared dealing with the occurrence of such crossings (CLAUSEN and GOODSPEED 1925, NEWTON and PELLEW 1926 and 1929, TSCHERMAK und BLEIER 1926, KARPECHENKO 1927, and others).

The present preliminary publication treats the investigations carried out at the Plant Breeding Station Øtoftegaard (belonging to the Co-operative Wholesale Society in Copenhagen and the Danish Co-operative Seed-Growers' Association in Roskilde) for the purpose in the work of plant breeding to try crossing of species for production of such new constant forms.

In the summer of 1928 artificial crossing was carried out between swede (*Brassica napus* L. var. *sativa rapifera*) and turnip (*Brassica campestris* L. var. *sativa rapifera*). For the crossing we used plants of the strain of swede »Lyngby Bangholm», which has oval root-form, red-violet head and yellow coloured flesh. Of turnip we employed plants of the kind »Yellow Tankard», which also has yellow coloured flesh but green head and longish root-form. The pollination was performed so, that the flower-buds were emasculated before the flowering and the pollen was at the same time brought on the stigmas, whereafter the inflorescence was isolated in caps of gauze. Cross-pollination was performed in both directions. We obtained positive results only from the crossing between three pairs of plants. The attained quantities of seeds were small, especially the crossing turnip × swede gave very poor result. We got only some few poorly developed seeds, from which we only obtained 2 F_2-plants. Otherwise the three plants of swede produced more and better developed seeds.

These small lots of seeds were sown out in the spring of 1929 for investigation of the F_1-generation, and we got 47, 48 and 66 plants resp.

The F_1-type was mainly intermediate. With regard to the leaves they took up an intermediate position between the parents, it is true, but they were a little more similar to swede than to turnip.

The form of the roots was intermediate too, being a half-long cone, and most of the plants were set with »crossing-knots» of differing size on the roots.

As to the head-colour all the plants of the two former progenies were red-violet, while the latter progeny segregated in 32 red-violet and 34 green-reddish plants.

Unfortunately there was not made cytological investigation on these F_1-plants, but such investigation was made beforehand on the two above mentioned F_1-plants from the crossing turnip $\times$ swede, and in these plants we found a chromosome-number of $2n = 28$, which just was the expected number, *Brassica napus* having $n = 18$ and *B. campestris* $n = 10$ (KARPECHENKO 1922), which results also have been confirmed by our investigations.

During the conservation through the winter of 1929—30 and after the planting-out in the spring of 1930 a good deal of the plants was lost on account of attack of diseases; the first mentioned progeny was quite lost and as to the other two we only got seeds from 23 and 32 plants resp. The plants were planted out into a green-house for self-pollination, and during the flowering season there was constantly made artificial self-pollination by hand.

The 55 plants yielded on an average 0,5 gr. of seeds per plant varying from quite few seeds to 2,7 gr., which latter quantity of seeds was harvested from plant no. 103. For comparison it can be stated that plants of swedes planted out under similar circumstances produced on an average 3,6 gr. of seeds per plant; thus we see that the F_1-plants were comparatively little fertile.

In the spring of 1931 the seeds in question were sown out for observation of the F_2-generation, and 50 samples out of 55 produced plants. After the harvest of the roots in these families the material consisted of 2368 F_2-plants, *i. e.* on an average 47 plants per family, but the number varied highly; from a single plant to 286, which number was counted in the family originated from plant no. 103.

On examination of the material all the families appeared to be offspring from hybrids. Generally there was a very pronounced segregation into different types. The segregation with regard both to the form and size of the leaves was well-marked, the variation was very great, but the main part of the plants was, regarding the type, more similar

to swede than to turnip, several plants being quite like swede in the leaves, but only a few had typical turnip-leaves. Also transgressive segregation was recorded, *e. g.* plants were found, which possessed leaves without any incisions at all, or without wax-cover, and moreover others with glistening smooth leaves.

Only a single progeny, no. 103, was characterised by a great constancy; the leaf-type was rather intermediate, and all the plants were of the same type, moreover the leaf-rosette was large and vigorous and early differed from those of the other families.

As to the form of the roots there was a well-marked segregation among the plants. After the harvest the roots were classified after their forms. We classified them in the following four groups: globular roots, oval roots, a half-long root-form and roots of a longish conical form. Thus we were able to classify 2274 roots in all.

Practically in all the families consisting of a fairly great number of individuals the segregation was so well-marked, that each family possessed roots in all the four groups, only in a few cases the variation was smaller. The family no. 103 showed the smallest variation. While the procentual distribution of the roots into the four groups with regard to the 49 progenies as a whole was 17—18—53 and 12 pCt. resp., the family no. 103 showed 0—0—84 and 16 pCt. resp. Thus we see that all the roots of this family had a half-long conical form, no one being globular or oval.

With regard to the colour of the heads there was also a distinct segregation in most of the families. Only in a part of the progenies originating from green-headed F_1-roots the colour was constant. In the family no. 103 all the roots were green-headed with a slightly reddish hue.

All of the observations mentioned above have shown that on essential points the family no. 103 behaved in a manner that differed from the other families. The F_1-plant was characterised by a relatively great fertility when self-pollinated and the F_2-generation, being of a rather intermediate type, showed on the different points great constancy. These facts indicate, that here we have a new constant species-hybrid! The cytological investigation (comp. part II) *has confirmed this supposition, and it has to be regarded as surely ascertained that a new amphidiploid species-hybrid has come up, and so* — named after the parental species — *it has got the name Brassica napocampestris.*

A closer investigation of the new species, *e. g.* of the reduction division and its behaviour when crossed back to the parental species,

besides investigations on material from the other highly segregating hybrid-families are intended, and when carried out information of the results will appear.

II. CYTOLOGY AND THEORETICAL CONSIDERATIONS.

(BY Ö. WINGE).

In order to be able to make a cytological investigation as soon as possible of the constant family originating from the highly fertile F_1-plant, no. 103, 5 roots were planted into flower-pots in August 1931, for the purpose of ascertaining the number of chromosomes in the cells of the root-tips.

This cytological investigation was performed at the Genetic Laboratory of the Royal Veterinary and Agricultural College in Copenhagen and showed, as expected, that the five plants had 56 chromosomes in the somatic cells, *i. e.* the sum of the somatic numbers of the parental species, *Brassica napus* having 36 chromosomes and *B. campestris* 20 in somatic cells.

Later on, 16 plants were potted in addition. The examination of these took place at the Laboratory of Øtoftegaard, and it fully confirmed the first observation. All the examined F_2-plants, 21 in all, originating from plant no. 103, possessed 56 or at any rate very near 56 chromosomes. Thus it is sufficiently certain that a new amphidiploid constant species-hybrid has arisen.

The question now rises, how the doubling of the chromosome-set came into existence, and concerning this there is no doubt at all. As already the fertility of the F_1-individual had been extraordinary, the F_1-plant itself must have had the doubled number of chromosomes, and obviously it had been doubled throughout, because the plant had no appearance of a chimera with diploid and amphidiploid parts of tissue; such a thing also would have involved that not all of the F_2-plants had been identical, for in the progeny of almost all the other F_1-plants segregation was well-marked, as mentioned above. The doubling of the chromosome-number in F_1 has probably taken place already at the first division in the zygote.

The details of this process are of minor importance; it is possible that the chromosomes of the primary nucleus have split in a stage similar to diakinesis, as has been shown in the tapetal cells of the anthers of *Humulus Japonicus* (WINGE 1917), and as LITARDIÈRE (1923) observed in the peribleme of *Spinacia oleracea*. A quite similar

phenomenon was found in the *Bacterium tumefaciens*-tumors of *Beta vulgaris* (WINGE 1927) and in tar-tumors of mice, *Mus musculus* (WINGE 1930). It is also possible that an ordinary division of nucleus has taken place so that a cell containing two nuclei has come out, and that these nuclei during a following simultaneous division have fused to one, as often happens in tapetal cells of the anthers, and in accordance with the hypothesis of WINKLER (1916) and the observations of JØRGENSEN (1927). Even other, perhaps less probable, contingencies could not be excluded.

At all events, *the constancy of the F_2-generation is obviously due to a somatic doubling in the F_1-plant and not to the formation of diploid gametes by a — for the rest — normal F_1-plant.*

Thus the new *Brassica napocampestris* has arisen in accordance with the scheme which I set up in 1917, in order to illustrate the origin of new species, and not as the tetraploid form of *Raphanus* × *Brassica* (KARPECHENKO 1924, 1927), which appears in the F_2-generation — and not earlier. In *Raphanobrassica* the F_1-individuals partly produce diploid gametes by a so-called semiheterotypic division (ROSENBERG 1917, 1926). As a whole, it holds good of the majority of the constant species-hybrids originated by crossing and chromosome-doubling that they probably have arisen by somatic doubling. Unfortunately, in this respect several misunderstandings have crept in, and also my hypothesis of 1917 has been wrongly interpreted, some authors having thought that the splitting of the chromosomes, which leads to »indirect chromosome binding» and thereby to the origin of new species, in accordance with my hypothesis was to take place at the reduction division in F_1, although I said explicitly that the F_1 itself had doubled chromosome number in its somatic cells. As to the F_1-hybrid I said, in 1917, p. 199: »If the chromosomes are to find a partner, then each of *the chromosomes in the zygote must divide* for thus indirectly to produce a union of chromosomes, and we must assume that *this is realized in the hybrid zygotes* which have possibility at all of propagating — in accordance with what we know from experience as to the behaviour of pairs of chromosomes. *The hybrid sporophyte thus produced will then have 4 x chromosomes taking the number of each of the parent gametes as x*».

The amphidiploid *Primula Kewensis*, *Rosa Wilsoni*, *Nicotiana digluta*, *Fragaria bracteata* × *F. Helleri*, *Solanum nigrum* × *S. luteum*, *Saxifraga Potternensis* and probably *Primula Bulleyana* × *P. Beesiana* behave in this manner. As to TSCHERMAK's *Aegilops* × *Triticum*

hybrids together with *Triticum turgidum* × *T. villosum* the circumstances are not known in all details. Thanks to the investigations of KIHARA and KATAYAMA (1931) it is proved that the doubled hybrid *Aegilops ovata* × *Triticum dicoccoides*, brought forward by these investigators, is due to a failing reduction division in F_1. TSCHERMAK's view (1929) that constant *Aegilops* × *Triticum* hybrids in all cases should have arisen from diploid gametes, produced in F_1, is, however, hardly correct.

In the cases where semiheterotypic division has been found, it takes place, as a rule, without much regularity, and often aberrant sterile forms are produced. Nevertheless it is sufficiently established that this type of division is the cause of the origin of some of the now known constant hybrids. Thus the constant species-hybrids *Phleum pratense* × *alpinum*, *Digitalis Mertonensis*, *Nicotiana tabacum* × *silvestris*, and *N. rustica* × *paniculata* have originated in that way.

SUMMARY.

Brassica napocampestris is a new instance of a constant hybrid or a new species originated by species-crossing and a subsequent total doubling of the somatic chromosomes in F_1. The doubling probably has taken place at the first cell-division in the zygote.

While the chromosome numbers of the parent species are $n = 18$ in *Brassica napus* and $n = 10$ in *Brassica campestris*, *Brassica napocampestris* has $n = 28$.

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SEGREGATIONS IN RED CLOVER (TRIFOLIUM PRATENSE L.)

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INTRODUCTION.

IN 1923 plant breeding work with red clover was started at Felleskjøpets Stamsedgård by the Late Dr. W. CHRISTIE which work has been continued from 1928 by the present author. A number of families have been inbred by brother-sister matings for some generations and descriptions have been made of a large number of single plants. In 1928 genetic experiments were started with the aim of studying the inheritance of a number of morphological characters. In both of these ways segregations of several characters have been noted and although the data are yet casual and not fit for a final analysis, they seem worthy of a preliminary report, especially as the accumulating of genetic data in red clover is a rather slow project.

From a purely genetic point of view red clover is not a favourable plant; it is a slow grower, gives only one seed per flower, is nearly selfsterile and suffers from inbreeding. On account of the constant cross-fertilization it is also extremely heterozygous, so that it is necessary to inbreed the material to obtain pure stocks before a safe analysis can be made. It is, however, a very important agricultural plant, and the breeding of red clover is one of the most important problems of plant breeders today. It therefore ought to be studied genetically and it is interesting to a geneticist on account of its enormous variability and favourable on account of its low chromosome number, $n = 7$ (H. WEXELSEN 1928).

The genetic experiments have been supported by a contribution from *1905-Fondet for landbruksforskning i Norge* for which I give my best thanks.

EARLIER WORK.

Little has yet been published on the genetics of red clover, but a few data are at hand from the observations of several investigators and some of these, concerning the characters reported on, will be briefly mentioned. KAJANUS (1912 a) found that the leaf spot was

formed in the following way: In a part of the leaf surface the cells of the epidermis grew more rapidly than the underlying pallissade cells. In this way a cavity filled with air was formed, the pallissade cells were exposed to stronger light and part of the chlorophyll destroyed. The white colour of the leaf spot is effected partly by the destruction of the chlorophyll, partly by the intercellular air. He assumed the presence of one factor for central and one for basal leaf spot. GMELIN (1914) assumed the presence of two factors for central leaf spot.

DE VRIES (1901) found that white flower colour was recessive to red and that F_2 segregated in the ratio 3 red : 1 white. KAJANUS (1912 b) also found white to be recessive to red. GMELIN (1914) found in one cross of red $\times$ white all offspring red flowering, in two other crosses he found 29 red : 29 white, and 155 red : 103 white. WITTE (1921) describes types of white flower colour combined with red stem and yellow seed, he mentions that it is difficult to be sure that there is no colour in the flower. He, however, also describes a type with white flowers and white seed, which he regards as a true albino for anthocyanine colour and the bottom recessive of colour types in red clover. Both KAJANUS and WITTE discuss the correlation between flower and seed colour and both find that white and very light flower colours are always combined with yellow seed (except the white seeded type). KAJANUS describes a type with blue flower colour which is recessive to red and always seems to be combined with orange brown seed.

DE VRIES (1901) found yellow seedlings in *Trifolium pratense* and the same has been found by several investigators working with red clover. Among 492 plants from selfing, KIRK (1925) obtained 41 chlorophyll defective seedlings of which 24 were albinos.

MATERIAL AND METHODS.

The material consists of plants selected for breeding or for genetic study almost exclusively from the Norwegian strain of late red clover, Molstad. In the breeding work isolation has been effected by enclosing the whole plant or part of the plant in a cage of cheese-cloth put on a frame of wire supported by two sticks. In the genetic experiments pergamine paper bags on single heads — also supported by a stick — have been used. The red clover material used has proved to be very highly selfsterile and emasculation has therefore not been regarded necessary. On 125 plants isolated in cages with about 166000 flowers unpollinated flowers have given 611 seeds, *i. e.* 0,36 % seed. However,

most of this seed was found on a few plants and often in a single head which indicated that they were not due to selfing, but to foreign pollen. Some of these »selfed» seeds were obtained in inbred, rather constant families, and the offspring proved that they were not due to selfing, but to pollen from another family. Some heads within each cage were cross-pollinated and it is probably during the procedure of pollination that some pollen has landed on not treated heads. For this reason bags on single heads were used in the genetic crosses and most of the segregations reported are from such crosses. 86 plants with 381 heads included in bags, comprising 19050 untreated flowers, gave 45 seeds. This is 0,24 % selfing in unpollinated flowers, but in flowers treated with pollen from another plant, the chances for selffertilization are of course smaller, because the foreign pollen tubes, as we know, have a much higher growth rate then those of the plants' own pollen. Selfing cannot therefore in any serious way have effected the segregations in this material. In general one cannot rely on red clover being completely selfsterile, as several investigators have found plants and strains that give a fair amount of seed by selfing (see SYLVÉN 1929). But if the plants are tested for their selfsterility one can use the non-castration method, except where some very critical question shall be decided.

LEAF SPOT.

The presence of a white spot on the leaves of *T. pratense* is regarded as a characteristic of the species, but in both wild and cultivated red clover plants without leaf spot are rather frequent. In table 1 are given the number of plants with and without leaf spot in a number of wild and cultivated strains of red clover. It is evident that plants lacking leaf spot are more frequent in wild Norwegian red clover than in the local cultivated strains, which is surprising in view of the fact that wild red clover is in general less variable and contains less recessive mutant types than the cultivated.

Leaf spot in red clover may be central or basal, in this report only the central leaf spot will be dealt with. In table 2 are given the segregations for leaf spot *versus* no leaf spot; in the lower part 9 crosses are listed showing a 1 : 1 segregation, total ratio: 188 with : 198 without. In the upper part one finds 9 crosses giving a 3 : 1 ratio; there is a deficiency of non-spot plants which is mainly due to the family 24—1. 1927 with a ratio of 58 : 5. This is probably a case of suppressed leaf spot in the 5 plants, the whole family being homozygous for leaf spot.

TABLE 1. *Number of plants without leaf spot in various strains.*

	Number of plants			Number of plants	
	with leaf spot	without leaf spot		with leaf spot	without leaf spot
Wild red clover:			Cultivated red clover:		
Vang, Hedmark...	27	19			
Valdres	49	22	a) Norwegian local strains:		
Etnestølen	21	15			
Sikkilsdalen.....	24	20	Molstad	149	27
	121	76	Leinum	57	2
%	61,42	38,58	Fosnes	27	2
			Toten	37	1
			Hove.....	46	4
			Bråta.....	40	6
			b) Other strains:		
			Östgöta I, Swedish bred.....	19	1
			Östgöta II, Swedish bred	19	1
			Sibirian	39	1
			Italian	20	—
				453	45
			%	90,96	9,04

As will be mentioned later, suppressors of leaf spot occur; the ratios obtained by GMELIN and interpreted on the basis of two factors for leaf spot are probably also of the same nature.

SIZE OF LEAF SPOT.

The leaf spot does not only vary in its presence or absence or in its position, but also in shape, size, intensity and colour. In figs. 1 and 2 are represented three types of size in leaf spot which has so far been isolated as constant characteristics of some inbred families, *extended*, *large* and *small*. They are all of the V-shaped type, but the arms may be more or less broken or shortened, especially in the small which often takes a triangular shape. Several families have given a sharp segregation for large *versus* small spot (table 3). The data show that there is one factor determining the differences between these two types.

TABLE 2. *Segregations of leaf spot versus no leaf spot.*

Family no.	Number of plants		
	with leaf spot	without leaf spot	total
51, 1926	62	18	80
24—1, 1927.....	58	5	63
51—1—1, 1928 ...	46	12	58
Kr. XIII 1931 ...	38	14	52
Kr. XIX » ...	40	19	59
A 32 » ...	17	4	21
A 40 » ...	20	10	30
A 52 » ...	16	3	19
A 53 » ...	42	11	53
	339	96	435
3:1 expected ...	326,25	108,75	435
6, 1926	56	73	129
11—1, 1927	28	18	46
6—2, »	31	27	58
48—1, »	17	11	28
6—1—1, 1928	5	7	12
51—1—1—1, 1931	20	19	39
A 38 »	6	7	13
A 39 »	18	25	43
A 48 »	7	11	18
	188	198	386
1:1 expected ...	193	193	386

TABLE 3. *Segregations of large versus small leaf spot.*

Family	Parent plants	Number of plants		
		large leaf spot	small leaf spot	total
1929				
86—1—2 ...	86—1^a × 86—1^b	22	22	44
A 12.....	86—1^e × 29—1^a	30	24	54
9—1—3 ...	9—1^e × 9—1^f	17	19	36
1931				
9—1—1—7	9—1—1^d × 9—1—1^e	22	22	44
9—1—1—5	9—1—1^d × 9—1—1^a	4	6	10
		95	93	188
	1:1 expected	94	94	188
1931				
A 31.....	G 30 × G 36	32	13	45
A 19.....	48—1^a × 32—1^a	16	2	18
A 18.....	48—1^b × 46—1^c	42	11	53
9—1—1—3	9—1—1^a × 9—1—1^c	19	8	27
9—1—1—2	9—1—1^c × 9—1—1^d	15	3	18
9—1—1—11	9—1—1^d × 9—1—1^g	35	14	49
Kr. XII ...	6—1^g × 64—1^a	49	7	56
Kr. XV ...	9—1—2^a × 9—1—1^a	42	20	62
Kr. XVIII	51—1—1^a × 78—1—2^a	53	14	67
Kr. XIX ...	51—1—1^d × 13—1—1^b	28	12	40
A 49.....	G 39 × G 22	21	5	26
		352	109	461
	3:1 expected	345,75	115,25	461

TABLE 4. *Extended leaf spot.*

Family	Parent plants	Number of plants			
		extented leaf spot	large leaf spot	small leaf spot	total
1931					
78—1—1—1...	78—1—1[a] × 78—1—1[b]	15	6	—	21
78—1—2—1...	78—1—2[a] × 78—1—2[b]	5	19	—	24
78—1—3—1...	78—1—3[a] × 78—1—3[b]	32	32	—	64
Kr. XVIII ...	51—1—1[a] × 78—1—2[a]	9	18	9	36

The distinction between large and extended is much less sharp, and classification in cases doubtful. In table 4 is given the classification

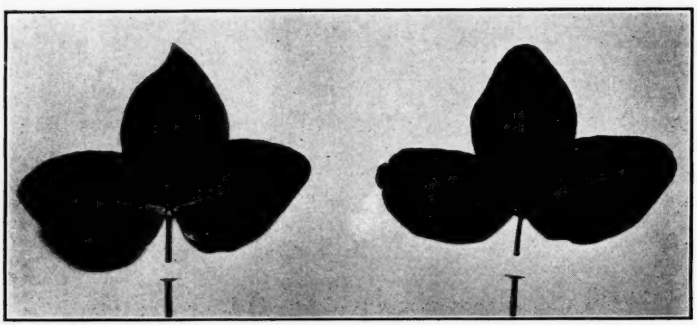

Fig. 1. Left no leaf spot, right small leaf spot.

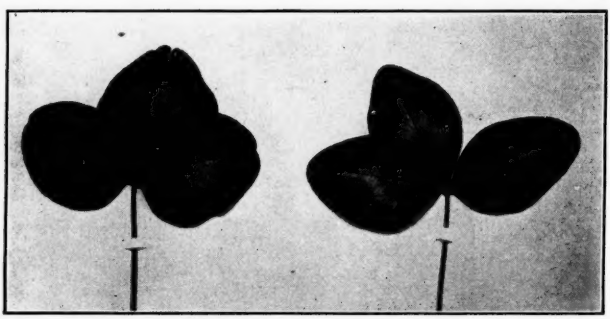

Fig. 2. Left extended leaf spot, right large leaf spot.

of some segregating families. The data are inconclusive, but indicate that extended is due to a modifier of large that is variable in its effect.

STRONG AND WEAK LEAF SPOT.

As mentioned before the spot may be more or less intense, in some plants only a faint trace of spot is found on a few leaves. One plant, 86—1[e] 1928, was studied carefully through one season and found to have no spot; its offspring, however, showed it to be genetically leaf spot and next season faint spots were found on some leaves. In another plant, G 27, no leaf spot was found in one season, but the offspring showed it to be heterozygous for spot; as it did not live next season,

TABLE 5. *Strong and weak leaf spot.*

Family	Parent plants	Number of plants		
		strong leaf spot	weak leaf spot	total
a) 1929				
86—1—2	86—1[a] × 86—1[b]	28	16	44
A 12.....	86—1[e] × 29—1[a]	27	27	54
1931				
A 26.....	G 21 × G 28	42	40	82
A 27.....	G 21 × G 27	37	34	71
A 38.....	G 36 × G 28	2	4	6
Kr. XII	6—1[g] × 64—1[a]	38	21	59
Kr. XIII.....	6—1—1[a] × 11—0—1[b]	25	24	49
Kr. XIV	9—1—2[b] × 54—1—1[a]	21	28	49
		220	194	414
	1 : 1 expected	207	207	414
b) 1929				
9—1—3	9—1[e] × 9—1[f]	29	7	36
1931				
A 37	G 3 × G 35	17	3	20
A 49.....	G 39 × G 22	18	8	26
		64	18	82
	3 : 1 expected	61,5	20,5	82
c) 1930				
A 18.....	48—1[b] × 46—1[c]	49	4	53
A 19.....	48—1[b] × 32—1[a]	17	1	18
A 21.....	48—1[b] × 46—1[a]	42	3	45
		108	8	116
	15 : 1 expected	108,5	7,5	116

reinspection could not be made. Heterozygotes for spot do not show less marked spot than the homozygotes. The weak spots represented in these segregations vary in degree of intensity, the consequence of the operating of at least 2 factors, nothing can as yet be said of the definite effect of each factor. Data on segregations are given in table 5. Eight crosses give a segregation of 220 strong : 194 weak, representing a 1 : 1 backcross ratio; there is a deficiency of weak, the deviation is, however, only 1,3 × the standard error.

Three families have given a 3 : 1 ratio of strong *versus* weak leaf spot, showing strong to be dominant, the numbers agree well with those theoretically expected. Finally three families, all involving crosses with plant 48—1^b, have given a segregation of 108 strong : 8 weak, which corresponds very nearly to a 15 : 1 ratio. The four plants involved apparently are heterozygous for two suppression factors.

COLOUR OF LEAF SPOT.

The colour of the leaf spot may be white or yellow, two families have segregated for this character:

		yellow	white
1931	6—1^g × 64—1^a	20	6
»	9—1—2^a × 9—1—1^a	12	4
		32	10

Yellow is dominant giving monofactorial segregation with white.

LEAF COLOUR.

Leaf colour has varied in this material from pale yellowish green to normal or medium, dark green and blue green. Although leaf colour is a striking characteristic of many inbred families, classification of segregating families is not easy. We find here a gradual transition from one grade to another and the leaf colour changes during the development of the plant, so one may find very different shades of colour on a single plant. In table 6 are listed the segregations for dark green and medium and for medium *versus* pale green, the characters being dominant in the order mentioned. Four families segregate 70 dark : 59 medium, clearly a 1 : 1 backcross ratio and one family 19 : 3, agreeing with a 3 : 1 ratio.

Five families segregate: 99 medium : 22 pale green, the numbers expected on a 3 : 1 ratio are 90,75 : 30,25, there is a deficiency of pale, the deviation is, however, not more than 1,7 × standard error.

Three families have given both dark, normal and pale in the following ratios: 26 dark : 136 medium : 15 pale green. This ratio is probably the result of the operating of two factors in heterozygous and

TABLE 6. *Leaf colour.*

Family	Parent plants	Number of plants with leaf colour			
		dark green	medium green	pale green	total
a) 1931					
78—1—1—1...	78—1—1[a] × 78—1—1[b]	11	6	—	17
78—1—2—1...	78—1—2[a] × 78—1—2[b]	13	8	—	21
78—1—3—1...	78—1—3[a] × 78—1—3[b]	30	25	—	55
Kr. XVII.....	6—1—1[a] × 3—1—1[a]	16	20	—	36
		70	59	—	129
	1 : 1 expected	64,5	64,5	—	129
b) 1929					
54—1—2	54—1[a] × 54—1[d]	19	3	—	22
	3 : 1 expected	16,5	5,5	—	22
c) 1929					
Kr. I	78—0[a] × 78—1[a]	—	14	5	19
Kr. III.....	78—1[g] × 54—1[b]	—	20	3	23
Kr. V	15—0[c] × 13—1[a]	—	18	6	24
1930					
A 1	G 1 × G 4	—	20	5	25
A 6	46—1[a] × 14—1[b]	—	27	3	30
		—	99	22	121
	3 : 1 expected	—	90,75	30,25	121
c) 1930					
A 17	32—1[a] × 14—1[a]	10	49	5	64
A 18	48—1[b] × 46—1[c]	12	46	7	65
1931					
Kr. XV.....	9—1—2[a] × 9—1—1[a]	4	41	3	48
		26	136	15	177

homozygous condition and as the class limits are not sharp, a calculation of the genic basis of the groups will be doubtful. Pale green is the most distinct type and taking this class by itself, we get: 162 : 15 which is very near a 15 : 1 ratio, indicating that pale is the double recessive type.

ANTHOCYANINE PIGMENT.

Red pigment is present in red clover on the stem, on the nerves of the stipules and involucre and as diffuse colour on both, in the calyx and corolla and in the seed. Plants lacking anthocyanine pigment have green stems, stipules, involucre and calyx and white flowers and seed. The production of red colour (and yellow in the seed?) is dependent on a basic colour gene, which of course also governs the production of colours representing modifications of red. One plant, G 12, without any red colour in the vegetative parts and with white flowers and seed, was crossed to a plant, G 3, with nearly white flowers, green stem, red stipules and violet seed. F_1 consisted of plants lacking all red pigment,

TABLE 7. *Anthocyanine segregations.*

Family	Parent plants	Formula of parent plants	Number of plants		
			with pigment	without pigment	total
a) 1931					
A 24	G 12 × G 3	*cc* × *Cc*	9	9	18
A 56	G 50 × G 51	*cc* × *Cc*	10	6	16
A 58	G 50 × G 52	*cc* × *Cc*	7	4	11
A 59	G 50 × G 54	*cc* × *Cc*	1	3	4
A 60	G 50 × G 53	*cc* × *Cc*	19	11	30
			46	33	79
	1 : 1 expected		39,5	39,5	79
b) 1931					
A 57	G 55 × G 56	*Cc* × *Cc*	21	10	31
	3 : 1 expected		23,25	7,75	31

plants with red pigment and nearly white flowers like G 3 and plants with normal red flowers. Leaving out for the present the white—pink flower colour, which is due to another gene, F_1 consisted of 9 with red pigment and 9 without, showing that G 3 is heterozygous for the colour gene for which G 12 is homozygous recessive. An F_1 plant, G 50, without red pigment (white seeded) was mated to 4 F_1 sister plants with red pigment and gave 37 red : 24 non-red, adding the F_1 the total backcross is 46 red : 33 non-red (table 7). A mating of 2 F_1 plants with pigment gave an F_2 of 21 red : 10 non-red. All non-red plants lacked colour in all parts of the plant, the backcross plants flowered too late to get the seed colour, but the white flowered plants in the cross G 12 × G 3 all had white seed.

RED COLOUR ON STEMS AND STIPULES.

The red colour on stems and stipules varies immensely both as regards distribution and intensity. Genetically it is apparently modified by intensifying, suppressing and distributing factors and it is also exceedingly sensitive to external conditions, especially the light. Plants grown densely together usually show but little red and for classification

TABLE 8. *Red colour on stems.*

Family	Parent plants	Number of plants			
		dark red	light red	green	total
a) dark red × dark red 1930					
A 7	14—1b × 48—1b	39	22	3	64
A 10	14—1a × 14—1b	14	4	2	20
A 11	14—1a × 48—1b	12	14	3	29
		65	40	8	113
	9:6:1 expected	63,57	42,37	7,06	113
b) dark red × green 1930					
A 6	14—1b × 46—1a	8	11	9	28
A 13	14—1a × 46—1a	2	8	14	24
A 18	48—1b × 46—1c	5	29	11	45
A 21	48—1b × 46—1a	2	16	14	32
		17	64	48	129
	1:2:1 expected	32,25	64,56	32,25	129
c) light red × green 1930					
A 1	G 1 × G 4	—	15	11	26
d) green × green					
A 2	G 3 × G 5	—	4	29	33
A 3	48—1a × 32—1a	—	5	34	39
A 5	G 3 × G 1	—	3	27	30
		—	12	90	102

purposes the plants must be widely spaced and not too luxurious. Even then classification is difficult and repeated classifications do not always give consistent results. The material has been examined 2 or 3 times and any plant showing at any time a trace of red has been classified as red. The colour varies from a very faint tint to a full dark red colour. The

red colour on stipules to a large degree follows the variations of stem colour, but they also vary independently of each other as will be mentioned later. As mentioned earlier *cc* plants have green stems, but also in *CC* plants pure green stemmed types occur. Some segregations from different crosses between various types of stem colour are listed in table 8. Crosses of dark red have given 65 dark red : 40 light red : 8 green, which agrees with the number expected if the dark reds are heterozygous for two factors for red, each alone giving light red and both combined dark red. The same plants are crossed to green (table 8 b) and have given the ratios: 17 : 64 : 48. Here are too many green and too few dark red, probably due to a poorer development of

TABLE 9. *Green stipules.*

		Number of plants		
		red	green	total
a) green × green 1930				
A 10	14—1a × 14—1b	—	22	22
	1 : 15 expected	1,33	20,67	22
b) green × red 1930				
A 7.....	14—1b × 48—1b	15	47	62
A 11	14—1a × 48—1b	2	25	27
		17	72	89
	15 : 49 expected	21	68	89
c) green × green (with green stem) 1930				
A 17	14—1a × 32—1a	4	12	16
	2 : 10 expected	2,67	13,33	16

colour in these families. Light red × green has in one cross given 15 light red : 11 green. Four crosses of greens have given 12 plants of a total of 102 with a slight tint of red on the lower part of the stem, probably we have not here to do with real anthocyanine colour, but with some other colouring of the skin.

As mentioned the colour on the stipules may vary independently of the stem colour, plants are found with intense red stems and completely green stipules and not only plants, but inbred families homozygous for this type. Likewise types are found with red stipule and green stems. Some crosses involving the first type are given in table 9. The data are yet too few to give a certain analysis, but they indicate that this type of green stipule is due to two dominant restriction factors.

FLOWER COLOUR.

There is a large number of flower colours and colour patterns in red clover. So far the following types have been recognized:

1. *All white.* — No trace of colour is found in the corolla at any time. Two plants of this type have been found in the original material, G 12 and G 13; both had completely green stems, stipules and calyx, but G 12 had white, G 13 violet seed. Crossed together they gave 25 plants, all with normal red flowers, which proves that the two types are genetically different. Both were also crossed to homozygous normal red and the offspring was all red flowered, showing that the two types

TABLE 10. *Flower colour.*

Family	Parent plants	Formulae of parent plants	Number of plants		
			white-pink	red	total
1931					
A 24 ...	G 12 × G 3	$Wp_3wp_3 \times wp_3wp_3$	2	7	9
A 42 ...	G 18 × G 2	$Wp_1wp_1\ Wp_2wp_2 \times Wp_1\ Wp_1wp_2wp_2$	12	8	20
A 29 ...	G 18 × G 16	» » × $wp_1wp_1\ Wp_2\ Wp_2$	6	3	9
A 39 ...	G 14 × G 16	$Wp_1wp_1\ Wp_3wp_3 \times$ » »	16	3	19
A 40 ...	G 15 × G 16	» » × » »	15	8	23
A 57 ...	G 55 × G 56	$Wp_3wp_3 \times Wp_3wp_3$	2	17	19

are completely recessive to normal. The crosses with G 12 are treated earlier, dealing with the segregations of the *c* factor for which G 12 is homozygous recessive (table 7). G 13 was also crossed to G 50, a *cc* plant from the cross G 12 × G 3, and the offspring was red flowered with red vegetative parts. G 13 is thus a recessive white, carrying *C*, but with a recessive gene w_1, causing white flower colour and probably also green vegetative parts.

2. *White with pink tube.* — The flowers are nearly white with a trace of pink on the tube. The colour is increasing with the age of the flower, spreading then over other parts of the flower. In the material 3 plants of this type were found, G 1, G 2 and G 16, all three had faintly red coloured stems, G 1 and G 2 had yellow-violet seed, the seed colour of G 16 was not ascertained on account of poor ripening. G 1 and G 2 were crossed and gave 36 plants, all with red flower colour; these two plants, although phenotypically indistinguishable, are therefore genotypically different. A red flowered F_1 plant, G 18 (table 10), was back-

crossed to G 2 and gave 8 red to 12 white-pink. In these the pink colour was stronger than in G 2, about of the same type as old flowers of this plant. The plants flowered late in the fall and the increasing cold weather seemed to increase the colour. The two genes present in G 1 and G 2 we may call wp_1 and wp_2. F_1 from the cross G 1 × G 2 was mated to G 16 and gave 6 white-pink : 3 red, showing that G 16 is either wp_1wp_1 or wp_2wp_2, as a later cross shows probably the former. G 1 was further crossed to normal red and gave all red flowering offspring. G 16 was also crossed to G 13 and F_1 consisted of 38 red flowering plants showing that these plants are genotypically different.

3. *White with pink tip.* — Nearly white flowers with a little pink on the tip of standard and wings; the colour is increasing with age, old flowers are therefore indistinguishable from flowers of type 2. At a young stage both are often completely white. Two plants of this type were found in the original material, G 3 and G 4, both with green stems, G 3 had red colour on the stipules and yellow-violet seed. G 3 was crossed to normal red and the offspring was all red flowered, the same result was obtained when G 4 was crossed to G 1, which shows that G 4 represents a recessive white-pink type different from G 1. F_1 from this cross was mated to G 2 and gave no white-pink offspring, proving that the factor in G 4 is also different from wp_2, there is thus a third gene causing white-pink flowers, wp_3. G 3 and G 4 have not been crossed, we may assume for the present that the same gene is operating in both as no data speak against this assumption. G 3 was crossed to the *cc* plant G 12 and the offspring segregated for white-pink, showing that G 12 was heterozygous for this gene. The segregations in backcrosses of white-pink are listed in table 10 with the formulae of the parents, the two types of white-pink are here listed in one column. Two F_1 plants from the cross G 1 × G 4 were mated to G 16 and gave the families A 39 and A 40 which segregated 31 white-pink : 11 red. This may be a 1 : 1 ratio, G 16 being homozygous wp_1wp_1 and otherwise homozygous dominant, but more probably it is a 5 : 3 ratio obtained if G 16 is heterozygous for wp_3. The total numbers will then be 26,25 : 15,75, which agrees better with the numbers actually found.

Other flower colours found in red clover are: pink, light rose, rose, or normal red, diffuse, purple and blood; a description of these types will be postponed till data on their inheritance are laid forth. The flower colours so far studied show very complicated relations and the plants are often heterozygous for several genes as is so often the case in red clover.

As mentioned before observations have been made by several investigators on the correlation between flower colour and seed colour. We have not yet obtained much data on seed colour, but a few points may be mentioned. Our white *cc* type has in all cases examined had white seed and corresponds to the white flowering, white seeded type of WITTE. The other white or nearly white flowering types have had yellow seed with more or less violet, which is in contradiction to the findings of KAJANUS and WITTE that such types always have yellow seed.

HEREDITARY RESISTANCE TO MILDEW (ERYSIPHE COMMUNIS).

The breeding material in the field has been more or less attacked by mildew in the fall; in 1930 the attack was especially severe and it was noted that there was a great difference between the families, some being completely white with mildew, while others, often by the side of the first, were completely free. Description of mildew attack was made and the results are listed in table 11. First are listed 4 families, 2 inbred and 2 outcrosses with only 1 plant of 166 not attacked by mildew. Next are given 6 families with 107 plants all free from mildew. The families were spread in duplicates over the field and the chances of infection should be equal; the differences between the families must be due to some inherent quality in them. It will also be noted that plants from family 6—1—1 are involved in all crosses giving susceptible families, whereas the resistant families have their origin from 54—1—1 and 9—1—1. In table 11^c are given the results of crossing plants from the resistant family 54—1—1 with plants from the susceptible 6—1—1 and 9—1—2, namely 68 attacked : 69 not attacked by mildew. Two other crosses have given the same kind of segregation, in all, these four families have given 111 attacked : 99 not attacked, agreeing with a 1 : 1 backcross ratio. Seven families have given a ratio of 205 resistant : 50 susceptible, probably a 3 : 1 ratio, the segregation was rather sharp and classification usually not doubtful. Three families have given a segregation of 126 resistant : 11 susceptible, agreeing with a 15 : 1 ratio. Plants nos. 9—1—1^a, 9—1—1^c and 9—1—1^d used in the last crosses are also used in 2 of the crosses in table 11^b giving all resistant plants, but the total numbers are only 29 and these families may therefore be segregating. Many plants have been used in more than one cross and behave consistently, but 3 families have given 119 attacked : 25 not attacked which do not fit into the given scheme. Many more diallel crosses are

TABLE 11. *Segregations for resistance to mildew (Erysiphe communis).*

Family	Parent plants	Number of plants: attacked by mildew	not attacked by mildew	total
a) 1930				
6—1—1—1	6—1—1[a] × 6—1—1[b]	27	1	28
Kr. XI.....	6—1—1[b] × 9—1—2[a]	81	—	81
Kr. XIII ...	6—1—1[a] × 11—0—1[b]	57	—	57
		165	1	166
	%	99,40	0,60	100
b) 1930				
54—1—1—2	54—1—1[c] × 54—1—1[d]	—	37	37
54—1—1—1	54—1—1[a] × 54—1—1[b]	—	19	19
9—1—1—2	9—1—1[c] × 9—1—1[d]	—	19	19
9—1—1—1	9—1—1[a] × 9—1—1[b]	—	17	17
9—1—1—4	9—1—1[b] × 9—1—1[e]	—	5	5
9—1—1—5	9—1—1[a] × 9—1—1[d]	—	10	10
		—	107	107
	%	—	100	100
c) 1930				
Kr. X	6—1—1[b] × 54—1—1[e]	38	47	85
Kr. XIV ...	9—1—2[b] × 54—1—1[a]	30	22	52
		68	69	137
Kr. XVII...	6—1—1[a] × 3—1—1[a]	22	13	35
Kr. XIX ...	51—1—1[d] × 13—1—1[b]	21	17	38
		43	30	73

Family	Parent plants	Number of plants: attacked by mildew	not attacked by mildew	total
d) 1930				
51—1—1—1	51—1—1[a] × 51—1—1[b]	7	38	45
78—1—1—1	78—1—1[a] × 78—1—1[b]	4	18	22
78—1—2—1	78—1—2[a] × 78—1—2[b]	9	17	26
78—1—3—1	78—1—3[a] × 78—1—3[b]	7	28	35
9—1—1—18	9—1—1[g] × 9—1—1[f]	5	15	20
Kr. XV.....	9—1—2[a] × 9—1—1[a]	11	61	72
Kr. XVIII	51—1—1[a] × 78—1—2[a]	7	28	35
		50	205	255
	1:3 expected	63,75	191,25	255
e)				
9—1—1—3	9—1—1[a] × 9—1—1[c]	4	33	47
9—1—1—7	9—1—1[d] × 9—1—1[e]	4	49	53
9—1—1—11	9—1—1[d] × 9—1—1[g]	3	44	47
		11	126	137
	1:15 expected	8,56	128,44	137
f)				
11—0—1—1	11—0—1[a] × 11—0—1[b]	37	8	45
64—1—1 ...	64—1[b] × 64—1[a]	24	10	34
Kr. XII ...	64—1[a] × 6—1[g]	58	7	65
		119	25	144

necessary to solve the question of the nature of the inheritance of resistance to mildew and studies must be made of the degree of attack and conditions of infection. The data clearly show, however, that resistance to mildew is an inherited character on a relatively simple genic basis.

We do not yet know whether mildew does serious harm on red clover. Under our climatic conditions it probably is not serious in the hayfields, but for the seed production it may be very harmful. WILLIAMS (1931) mentions that red clover plants under glass are very badly attacked by mildew, which reduces the seed setting and may even kill the plants.

OTHER HEREDITARY CHARACTERS IN RED CLOVER.

In the inbred material several more or less abnormal characters have cropped out which are worth describing. In most cases they probably represent the segregating out in homozygous condition of a recessive gene present in heterozygous state in the original material.

Abnormal seedlings. — Most of these have been chlorophyll deficiences which have been very common. They have not been much studied and many segregations not noted. It may be of interest, however, to note some of the types found.

Yellow seedling. — The cotyledons are of a clear yellow colour, the seedlings die when the nourishment of the seed is used. The type is quite common; 3 families have segregated 37 green : 9 yellow, apparently a 3 : 1 ratio and 2 families 35 green : 2 yellow, which indicates a 15 : 1 segregation.

Yellow green. — The cotyledons are of a yellowish green colour, later turning green. One family segregated 53 green : 21 yellow green, apparently the segregating out of a single recessive gene.

White spotted or mosaic. — The cotyledons have white spots mosaically arranged, some seedlings being all white. This is the only case in which pure white seedlings have been found. Two families segregated for this character, giving 42 green : 5 white spotted and 25 green : 2 white spotted which indicate in both a 15 : 1 segregation, the total ratio being 67 : 7 whereas we should expect $62{,}375 : 4{,}625$.

Yellow spot. — The cotyledons have a large yellow spot in the center. The type was found frequently in a material obtained from Prof. L. E. KIRK, consisting of single plant selections from the strain Sask. 319.

Fig. 3. Minute plant.

Fig. 4. Leaves and flower head of Minute plant.

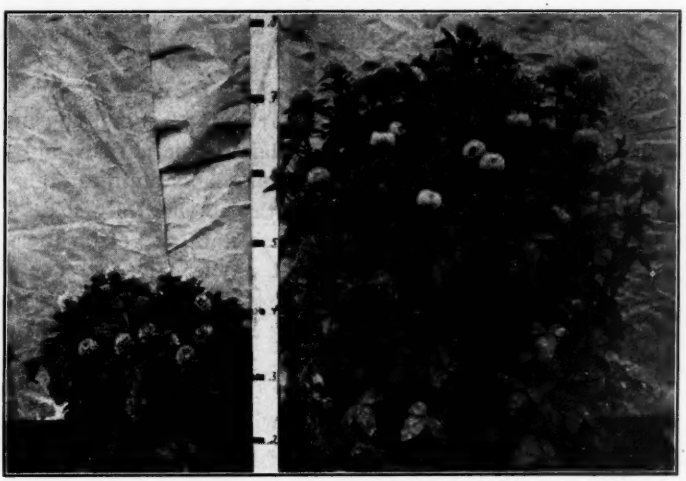

Fig. 5. Left dwarf plant, right normal sister plant.

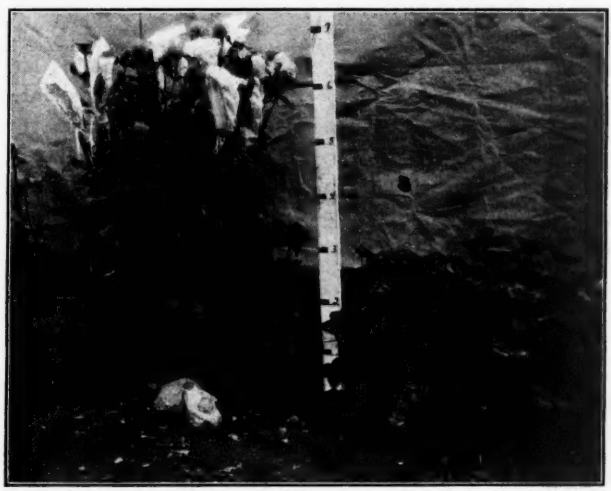

Fig. 6. Left normal plant, right stemless sister plant.

»*Minute*». — This type is called so on account of the very small leaves in the upper part of the plant. It segregated out in the family 11—0—1—1 which was the result of taking open pollinated seed from plant no. 11, mating two halfsister plants and in the next two generations mating sister plants. The family resulting from the last mating consisted of 38 normal plants showing the characters of the parents and 7 abnormal Minute plants. They were vigorous plants and desirable from a breeding point of view, with erect growth and fine leafy stems. The leaves on the lower part of the plant were normal, but on the upper part they were very small and with short petioles (fig. 3). The plants flowered very late, the normal plants of the family started to flower July 4 and were at the height of flowering July 18, but the first flowers on Minute plants were noted August 27. The heads were branched, with only 10—20 flowers of white colour (fig. 4). The Minute type is thus a complex of characters, none of which had been noted in the generations before. It may also be due to the segregating out of a single recessive gene, the ratio obtained corresponding fairly well to a 3 : 1 ratio. Its complex character may, however, favour the assumption that we do not have a single point mutant, but some other genotypical change. The pollen appeared to be normal, no seed was obtained as the plants flowered too late.

Dwarfs (fig. 5) were obtained in one inbred family and one cross between inbred families in ratios: 23 normal : 3 dwarfs and 39 normal : 4 dwarfs.

Plants without stems (fig. 6). — In one family plants lacking all flowering stems were found in the ratio 20 normal : 10 stemless.

Triple-head. — Two flower heads tight together on short stems is a common character in red clover. Triple-head is a peculiar type with three heads together on about 1 cm long peduncles, the heads were small and somewhat flattened. The type appeared in three families in the following ratios:

	normal	triple-head
A 56	11	1
A 57	27	1
A 60	22	8
	60	10

The character was very constant, appearing in all heads of triple-head plants.

SUMMARY.

1. The presence of a central leaf spot in red clover is determined by one dominant factor.

2. Three sizes of leaf spot are described, extended, large and small; small is recessive to large, and extended is a modified large.

3. The leaf spot may be more or less intense by the operation of at least two factors.

4. Leaf spot colour may be yellow or white, yellow is dominant and segregates with white in a 3 : 1 ratio.

5. Pale green, medium green, dark and bluish green leaf colours have been found. Dark, medium and pale are dominant in the order mentioned and the difference in each case apparently due to one factor.

6. Plants recessive for the colour gene *cc* form no red pigment and have green vegetative parts and white flowers and seed.

7. Red pigment on stems and stipules are conditioned by two dominant factors, giving a variation from a faint red tint to full dark red. The red colour is very sensitive to external conditions and classification difficult. Special restriction factors may give green stipules combined with dark red stems and *vice versa*.

8. White flower colour may be determined by the *cc* factor, but also by a recessive gene w_1, which is apparently not a basic colour gene. Two factors wp_1 and wp_2 have been found to produce white flower colour with a trace of pink on the tube, and one factor wp_3 to give white flowers with a little pink at the tip. Crosses between all these types give normal red flower colour.

9. Inbred families and F_1 crosses between such families have shown differences in resistance to mildew (*Erysiphe communis*), some being completely susceptible, others not attacked at all. Crosses between such families have segregated for this character.

10. Some chlorophyll deficient seedlings cropping out in inbred families are described.

11. In one inbred family a peculiar type, called Minute, has segregated out. In contrast to the normal plants of the family Minute was characterized by small leaves on short petioles on the upper part of the plant, very late flowering, branched heads with a few white flowers.

12. Dwarfs and plants without any flowering stems were found in some families.

13. A type has segregated in one family called triple-head with three flower heads together on elongated peduncles.

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RESULTS FROM A CROSS CABBAGE × SAVOY CABBAGE

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INTRODUCTION.

IN the year 1919 some crosses were made between a couple of cabbage varieties and a variety of Savoy cabbage. The scope of these crosses was to breed new cabbage varieties and the work was mainly done as practical breeding. This explains why several measurements were not taken and why the notes are not detailed, although it would have been very important for the theoretical evaluation of the results, had this been done.

The whole work was done during the time I was head of the vegetable experimental station at Alnarp. When leaving that situation I hoped that my new occupation should give me time to carry out some properly planned theoretical work with similar crosses. Therefore the publication of the results was delayed. However, it is now evident that in the next years I will have to devote my time to other problems and therefore it is considered appropriate to publish the preliminar results, since they still may be of some value for the breeding work.

MATERIAL.

LUND and KJAERSKOU (1885) place the Savoy cabbage and the common cabbage as different varieties of *Brassica oleracea* L., respectively var. *sabauda* DC. and var. *capitata* DC. KRISTOFFERSON (1924) is inclined to consider the Savoy cabbage as a sub-variety of *capitata*. This taxonomic question will be discussed later. Here, however, the most important differences between the two types may be stated.

The leaves of the common cabbage are slightly wrinkled and generally coated with a rather thick layer of wax. Those of the Savoy are deeply wrinkled and with few exceptions less waxy on the surface than those of the var. *capitata*. Following the differences in the wrinkling of the leaves the heads of the Savoy are much more loosely built than those of the common cabbage. The storing qualities of the head partially depend on its tightness. Thus the heads of the common

cabbage will keep much better than those of the Savoy when stored during the winter. In cold resistance the heads of the Savoy are on the whole superior to those of the common cabbage. The common cabbage contains some organic sulphur compounds which give it the special cabbage taste. The Savoy has very little or none of these cabbage taste substances. (The aim of the crosses here discussed was in fact to combine the storing qualities of the common cabbage with the delicate taste of the Savoy.) Even the rather rough chemical analysis which is possible in general agricultural and horticultural field experiment work reveals some distinct differences in the chemical com-

TABLE 1. *Average content of different substances in varieties of Brassica oleracea L. Per cent of fresh weight.*

Variety	Dry matter	Sugar	Reducing sugars	Crude protein	Crude fibre	Ash	Crude fat	Nitrogen free extract
Cabbage ...	7,83	3,76	3,24	1,53	0,67	0,62	0,073	1,18
Savoy	10,24	2,82	1,29	2,68	1,01	0,87	0,102	2,84
Brussels ...	13,56	2,72	1,39	5,46	0,99	1,09	0,273	3,01
Kale	18,16	2,06	1,62	5,79	1,79	2,00	0,660	5,87

position of the heads of the cabbage types here discussed. Table 1 (reprinted from LAMPRECHT, 1925) demonstrates the differences between Savoy and common cabbage as well as those between the other main varieties of *Brassica oleracea* with exception of the cauliflower.

The several commercial varieties used for the crosses may briefly be described as follows.

Cabbage, Amager Hunderup: late winter cabbage; sligthly wrinkled leaves which are greyish blue from a thick layer of wax; pear-shaped head; tall stem; one of the best cabbage varieties for keeping; leaves are hurt at — 4°/— 5° C.

Cabbage, Amager Marslev: late winter cabbage; leaves as Amager Hunderup; head ball-shaped and a little flattened; keeps very well in storage; leaves stand frost to about the same extent as those of Amager Hunderup.

Cabbage, Köpenhamns torg: early summer cabbage; leaves slightly wrinkled with rather thin wax coating; heads ball-shaped and very little flattened; does not keep well in storage; leaves are severely hurt already at — 1°/— 2° C.

Savoy, Vertus: somewhat earlier than Amager Marslev; leaves tightly covered by small, deep wrinkles; heads rather loosely built, ball-shaped but fairly flattened; does not keep in storage but will stand frost to — 5°/— 7° C.

Savoy, New year: very late winter-variety; leaves with small but very numerous wrinkles with a thick wax layer; head nearly ball-shaped, rather firm; does not stand storing well, but will stand — 10° C without damage even for fairly long periods.

In 1919 flowering plants of cabbage Amager Hunderup and Amager Marslev were available at Alnarp. All Savoy heads had been killed during the winter storage and therefore it was necessary to bring some flowering branches of Savoy cabbage from Denmark. The material available was of the variety Vertus. In 1923 some other crosses of the same kind were made involving among others the varieties Köpenhamns torg (cabbage) and New year (Savoy).

METHODS.

The seeds were sown in rows in specially prepared, good soil and the young plants were transplanted to their definite place in the fields when they reached a height of about 10 cm. Manuring, watering and other treatment was equal for all plants compared. Groups of plants of the parent varieties were grown in several places among the descendants of the crosses.

Crossing and selfing of the plants was made under pergamyne paper bags about 11 × 25 cm. The flowers to be crossed were emasculated one or two days before pollinating. The flowers isolated for selfing were generally left to themselves, although in some cases special care was taken to pollinate them with their own pollen.

RESULTS.

THE F_1 GENERATION.

Three different F_1 families were investigated. They may all be described as rather homogeneous compared to common cabbage varieties. The F_1 of a cross between two commercial varieties was in fact not more heterogeneous than any good cabbage variety and it gave the impression of being a little less heterogeneous than most of the Savoy varieties at that time. The homogeneity may partly be due to the fact that the F_1 generally descended from some few parent plants and that those were

selected as typical of the variety. The general impression of the several F_1 families was also that they represented a type intermediate between the parent varieties.

As to wrinkledness of the leaves the Savoy distinctly prevailed.

The waxiness of the leaves seemed a little more variable than it is in a good strain of cabbage. It was always intermediate between the parent types.

The firmness of the F_1 heads was intermediate between the parent types but the type with the more loosely built heads, the Savoy, prevailed somewhat.

Also in earliness the F_1 was intermediate but generally the early parent type showed incomplete dominance over the late one. Thus the F_1 of the cross cabbage, Köpenhamns torg × Savoy, New year was only a little later than Köpenhamns torg, although New year is very much later than that variety. In some other crosses, not further mentioned here, where the parental types were about equal in earliness, the F_1 was clearly earlier than any of the parents. This is best interpreted as an effect of the dominance of earliness over lateness.

The taste of the F_1 was a combination of the good characteristics of the parent types: it was juicy as that of the cabbage but absolutely lacking the aforementioned cabbage taste substances, thus demonstrating exactly the features desired in the new variety to come. As far as it may be considered appropriate to speak of dominance in characters of a so complex genic nature as these, it might thus be said that the juiciness of the cabbage and the delicate taste of the Savoy dominated.

In storing quality and in resistance to frost the F_1 was intermediate between its parents.

When selfed as well as when openly pollinated the F_1 plants showed a remarkable fertility which seemed to be decidedly better than the fertility of any of the parental races.

In weight of head (and also in volume) the F_1 plants were distinctly superior to their parent types. In 1920 the average weights pro head were: Amager Hunderup 2,7 kg, Amager Marslev 3,1 kg, Vertus 2,1 kg, and the average of all F_1 plants between the two cabbage varieties and the Savoy was 4,9 kg. From 1924 it may be sufficient to mention the results from the cross Köpenhamns torg × New year: Köpenhamns torg 3,3 kg, New year 1,7 kg, F_1 3,8 kg. The cabbage × Savoy hybrids thus are much more vigorous than their parent types.

Any commercial cabbage or Savoy strain is genically very heterogeneous and it would scarcely be possible to find two plants with the

same genic constitution within such a strain. It is therefore to be expected that F_1 families derived from different pairs of parent plants will show distinct differences. This was also very evidently the case in the crosses here discussed. In 1920 there was only made a general

TABLE 2. *F_1 families from different pairs of plants of Köpenhamns torg and New year.*

No. of *P*-plant Köpenhamns torg (Mean weight 3,3 kg)	No. of *P*-plant New year (Mean weight 1,7 kg)		
	8 : 1	8 : 4	8 : 5
12 : 1	Very early; firm heads 4,29 kg	Very early; fairly firm heads 4,58 kg	Fairly early; fairly firm heads 3,98 kg
12 : 2	—	—	Late; loose heads 2,74 kg
12 : 4	Heterogeneous in earliness; loose heads 3,84 kg	Heterogeneous in earliness; loose heads 4,06 kg.	Rather late; loose heads 3,55 kg

note of the obvious fact. In 1924 the F_1 plants as well as the comparable plants of the parent strains were weighed. Table 2 gives the results of these investigations.

THE F_2 GENERATION.

The differences in F_1 between the different families as well as between different plants within a family must to no small extent be caused by genic differences, since the parent plants were genically different and also heterozygous. These facts make it obvious that in breeding cross-fertilizing species the selection work should set in already in F_1 and not be delayed unto F_2. In accordance with this point of view a selection was made in F_1 and no F_2 grown from the inferior F_1 families. Equally, only the best plants of the good F_1 families were continued into F_2.

Several of the flowering F_1 plants were successfully selfed. From these selfed plants 780 F_2 plants were grown in 1922. From the seeds from open pollination about 1200 plants were raised. Since the F_2 plants from the selfings are the only ones of interest here, only these will be considered in the following.

No attempt was made to analyse the segregation in the different morphological characters. It might only be briefly stated that the segregation in all the characters considered under the F_1-description was obviously quantitative and fairly complicated. Still, among the 780 plants about 10 were judged to have the same low degree of wrinkling of the leaves as the cabbage parent. This would mean that not too many factors for wrinkling were segregating in these crosses in spite of the fact that the differences between the parent types were rather great.

The taste of the inner leaves of the heads was naturally of special interest, since the whole work was made in order to breed a race of a certain taste. The taste was tested in the following manner. With a knife a cut was made in the head and some pieces of the inner, etiolated leaves were tasted without cooking. A series of these tests showed that a great variation in taste was to be found among the F_2 plants. It was, however, equally noticeable that the main body of the plants tested came near to the taste of the F_1 type. No plants were found with the cabbage taste so accentuated as in the common cabbage used for parent in the crosses.

Because of too much other work it was impossible to weigh all the F_2 heads. Some knowledge concerning the weight of the F_2 may, however, be derived from the following facts. 166 heads were selected for propagation. The firmness of the head and its size were thereby mainly taken into consideration, and no head of weight below the average of the F_2 was selected. The average weight of the selected heads was 2,0 kg and the averages for nearby grown heads of Amager Hunderup was 1,8 kg and of Amager Marslev 2,2 kg. From these figures may assuredly be concluded that the F_2 heads at the best weighed as much as the average of the cabbage races used for parents. When this result is compared with the fact that the F_1 weighed considerably more than the best of the parents it is obvious that the inbreeding of the very vigorous F_1 has brought about a considerable decrease in weight.

The fertility of the F_1 was, as already mentioned, markedly greater than the fertility usually found in cabbage and Savoy cabbage. It was my intention to study the fertility of the F_2 rather thoroughly but an accident made that impossible. 72 of the 166 selected plants survived the winter in good shape and were planted in one seed plot. When their flowering stalks just were shooting they were, however, mostly destroyed by a very severe storm. Only three of them survived and the material available for further investigations was limited to these

three plants, all of them descendants from the cross Amager Hunderup × Vertus. They were selfed and crossed in bags. In all 278 flowers were selfed and in this case care was taken to open the bags several times during the flowering period and to bring about an artificial pollination. In spite of this precaution the 278 selfed flowers gave only 6 seeds. 88 flowers within the group of plants were crossed and all possible combinations were represented. These crosses resulted in 1445 seeds.

It is evident from the facts mentioned above that the sterility of the F_2 plants was a typical selfsterility and it should be classified as a parasterility according to the terminology of BRIEGER (1930). In 1920 selfings had been made on the cabbage parent plants of the cross. None of these had shown any marked selfsterility. The Savoy parents were in this respect unknown, since they were grown in Denmark. My experience from other work in cabbage and Savoy cabbage makes this a very extraordinary case because none of about 150 selfed plants in these types has shown such a high degree of selfsterility. The unlucky scarcity of the material makes the seeking for an explanation to pure guess work. Still it seems that degeneration accompanying the inbreeding might be the most probable explanation of the selfsterility in the F_2.

THE F_3 GENERATION.

Six selfed F_3 seeds were the whole result of the selfing of the three F_2 plants. These seeds were naturally most carefully treated and five of them germinated. However, the five young plants were all more or less abnormal. The best one of them had one and a half cotyledon, the others had only one or only part of one cotyledon. None of the five plants survived long enough to reach the state when it could be transplanted.

From the numerous seeds from crosses between the three surviving F_2 plants nearly 1000 gave plants and 600 of these were transplanted. Among these were progenies of the three possible combinations of the F_2 plants. The F_2 plants had been selected for the same morphological type and the three families were also rather alike. Still, they were evidently different in several minor characters. The common type to which they belonged was one intermediate between the original parents although with heads decidedly firmer and leaves less wrinkled than the F_1 type. The heterogeneity within the families was not greater than within any average-good cabbage or Savoy strain. The keeping

qualities of the F_3 as well as its frost resistance, however, were below the limits for what could be used for further breeding. Because the whole F_3 generation was produced in the haphazard manner described above it was considered not worth the while to continue the work with this material.

It might, however, be added that from the new crosses made in 1923 my successor at Alnarp, Dr. H. LAMPRECHT, by family-breeding has bred a quite new type of cabbage which well fullfilles the hopes placed on the original cross in combining the generally good qualities of the common cabbage with the delicate taste of the Savoy cabbage.

THE INBREEDING DEGENERATION.

The rapid dropping off of the vigour of the plants originating from selfings of different generations can scarcely be interpreted as anything but the result of the inbreeding. Such results of inbreeding are since long well known to the geneticists and are now generally explained on the basis of the dominance theory. Dr. K. B. KRISTOFFERSON has, according to an oral communication, had some of the same experience of high sterility of the F_2 in cabbage as the one reported above. One trait of the result should, however, be noted in spite of the fact that the material is not worthy of a thorough discussion of the matter: the depression from F_1 to F_2 is a fairly little one but the depression from F_2 to F_3 is a very great one. This is not quite in accordance with the expectation from the dominance theory of inbreeding depression. By taking into consideration the effect of homomeric factors it might, however, easily be brought in agreement with that theory, but this question will be considered in a special paper.

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